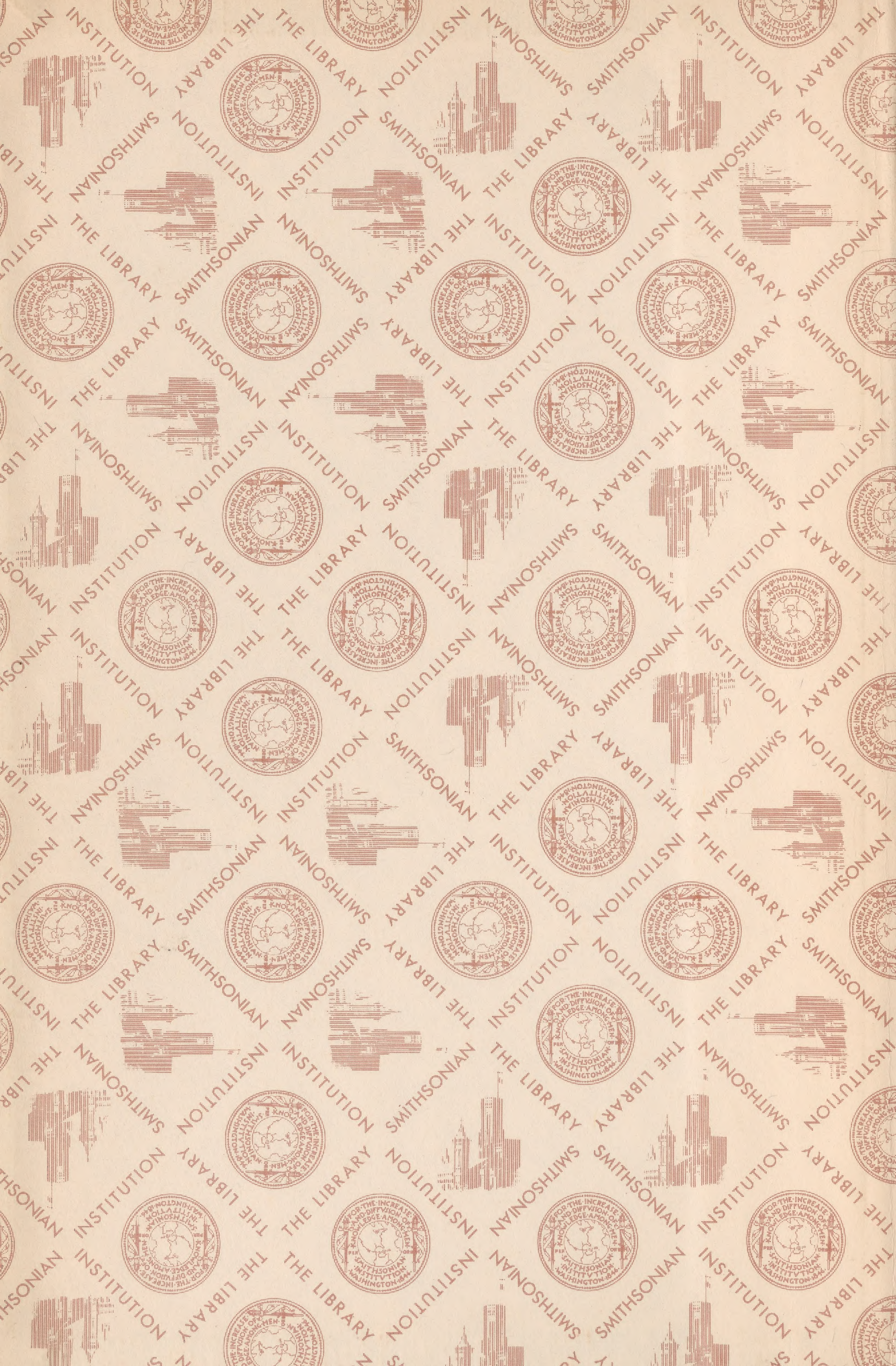
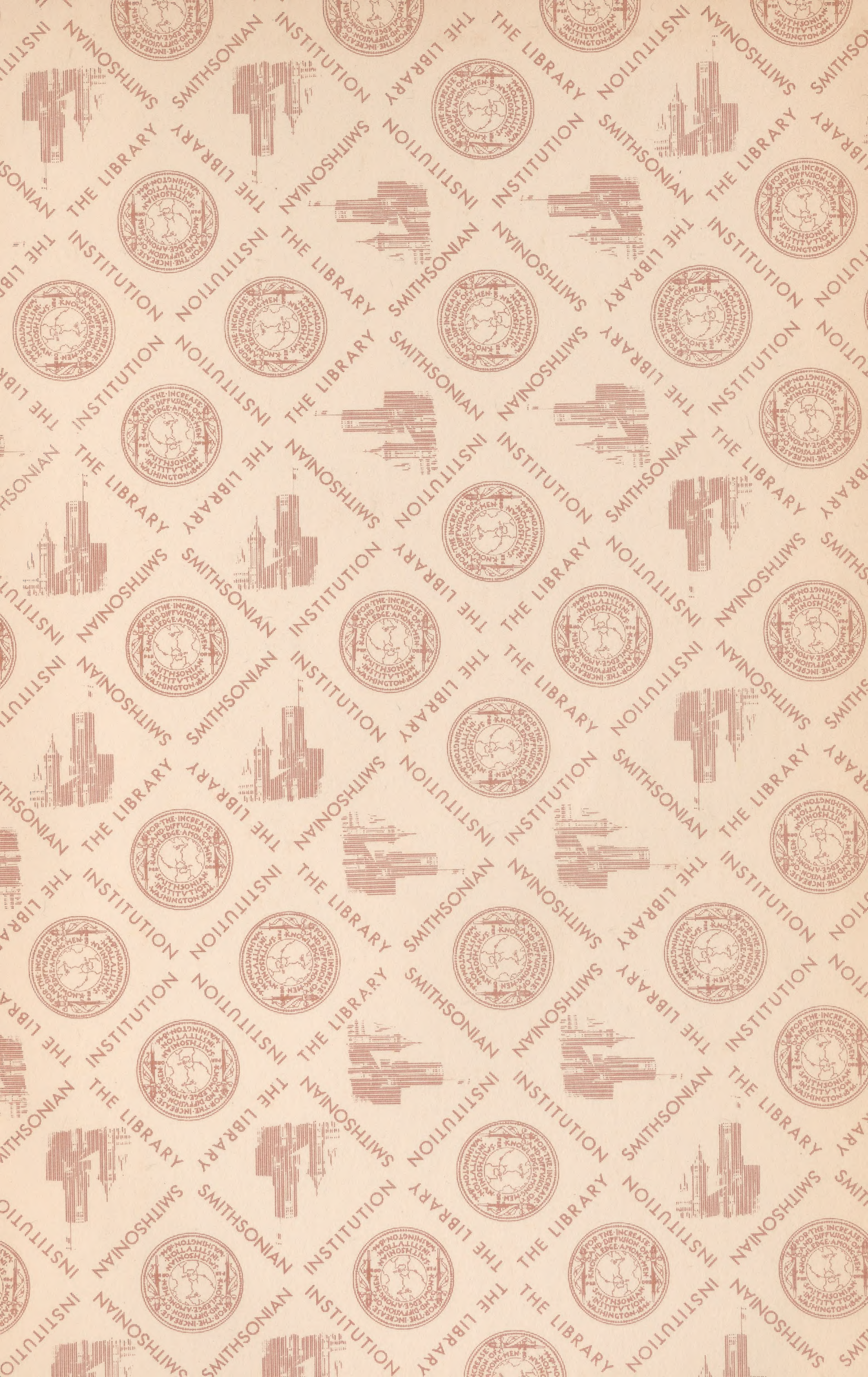






















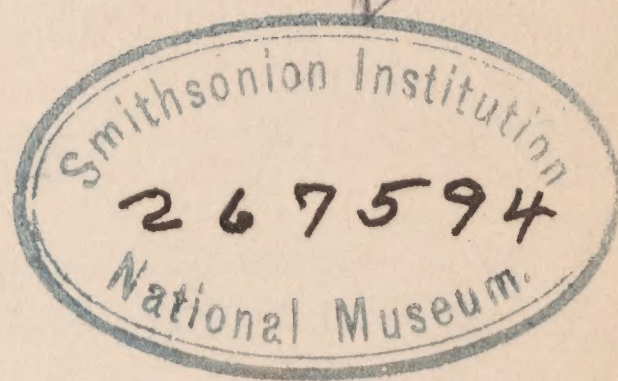
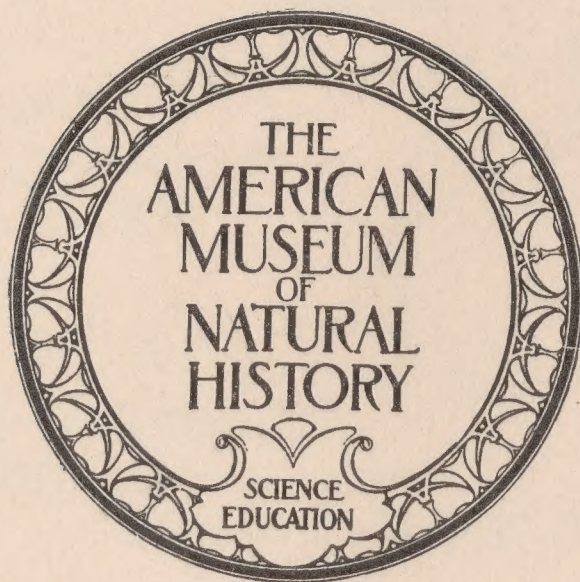




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ERRATA

- Page 12, line 1 from top, for *Ægialites* read *Ægialitis*.  
“ 93, (d), in caption, for *Peichærus* read *Perchærus*.  
“ 458, line 1, for ascalatboid read ascalabotoid.  
Pages 462 and 478 are incorrectly numbered.







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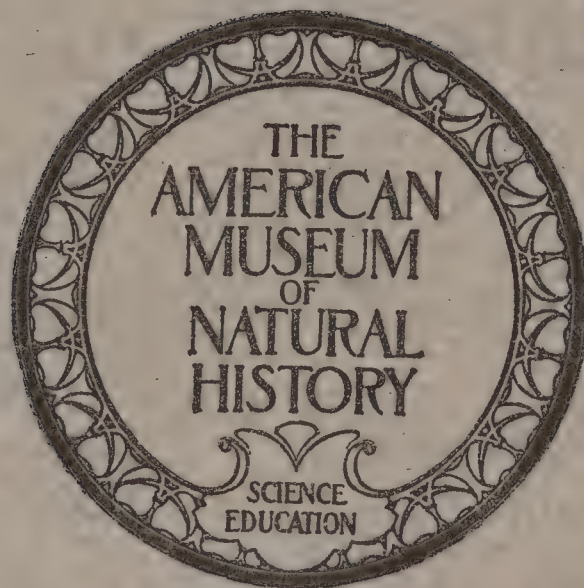
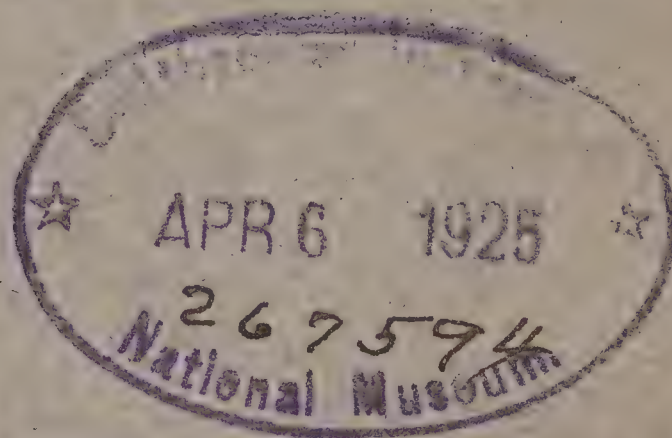
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Tiburon Island Towhee  
*Pipilo fuscus jamesi* Townsend



BULLETIN  
OF  
THE AMERICAN MUSEUM OF NATURAL HISTORY

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VOLUME XLVIII, 1923

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59.82(72.2)

**Article I.—BIRDS COLLECTED IN LOWER CALIFORNIA**

BY CHARLES HASKINS TOWNSEND

PLATE I

During the voyage of the U. S. Fisheries Steamer 'Albatross' in Lower California waters in 1911, collecting parties were sent ashore at thirty different points on the lower part of the peninsula, on islands in the Gulf of California and along the west coast. Among the collections were 804 birds representing 159 species and subspecies. As more than three-fourths of these were land birds, many of them peculiar to Lower California, and as certain islands had not previously been visited by naturalists, the collection is of considerable interest.

With the exception of those from Guadalupe Island, all of the birds taken were from points south of the San Benita Islands in the Pacific and Angel de la Guardia Island in the Gulf, a section including the lower half of the peninsula, and embracing all of the Cape faunal district. Specimens were obtained of most of the species characteristic of this district which lies within the arid tropical life zone.

The expedition being engaged in several lines of inquiry, including fishery and oceanographic work, and the duration of the voyage limited to two months, the time available for bird collecting was not sufficient for any very thorough examination of the bird fauna. The total number of days or parts of days spent at anchor was forty-three, but at some points the vessel remained at anchor only a few hours.



Following is a list of the anchorages, with dates of arrival and departure:

| PORTS VISITED                  | ARRIVAL | DEPARTURE |
|--------------------------------|---------|-----------|
| San Francisco.....             |         | Feb. 23   |
| San Diego.....                 | Feb. 25 | Feb. 28   |
| Guadalupe Island.....          | Mar. 2  | Mar. 4    |
| San Diego.....                 | Mar. 6  | Mar. 7    |
| San Benito Ids.....            | Mar. 9  | Mar. 10   |
| Cerros Island.....             | Mar. 10 | Mar. 12   |
| San Bartolome Bay.....         | Mar. 13 | Mar. 15   |
| San Cristobal Bay.....         | Mar. 15 | Mar. 15   |
| San Roque Id.....              | Mar. 15 | Mar. 15   |
| Abreojos Anchorage.....        | Mar. 16 | Mar. 16   |
| Santa Maria Bay.....           | Mar. 18 | Mar. 18   |
| Magdalena Bay.....             | Mar. 18 | Mar. 19   |
| Margarita Island.....          | Mar. 19 | Mar. 20   |
| Marcy Channel.....             | Mar. 20 | Mar. 21   |
| Cape San Lucas.....            | Mar. 23 | Mar. 25   |
| San Jose del Cabo.....         | Mar. 25 | Mar. 26   |
| Pichilingue Bay.....           | Mar. 27 | Mar. 30   |
| San Josef Island.....          | Mar. 30 | Apr. 1    |
| Agua Verde Bay.....            | Apr. 1  | Apr. 2    |
| Carmen Island.....             | Apr. 2  | Apr. 3    |
| Mulege.....                    | Apr. 4  | Apr. 5    |
| Concepcion Bay.....            | Apr. 5  | Apr. 8    |
| San Francisquito.....          | Apr. 9  | Apr. 10   |
| Angel de la Guardia Id.....    | Apr. 10 | Apr. 11   |
| Tiburon Id.....                | Apr. 11 | Apr. 13   |
| San Esteban Id.....            | Apr. 13 | Apr. 14   |
| Guaymas.....                   | Apr. 15 | Apr. 15   |
| Santa Catalina Id.....         | Apr. 16 | Apr. 16   |
| Santa Cruz Id.....             | Apr. 16 | Apr. 16   |
| Pichilingue Hbr. (La Paz)..... | Apr. 17 | Apr. 19   |
| Espiritu Santo Id.....         | Apr. 19 | Apr. 19   |
| Ceralbo Island.....            | Apr. 19 | Apr. 19   |
| San Jose del Cabo.....         | Apr. 20 | Apr. 20   |
| San Bartolome Bay.....         | Apr. 23 | Apr. 23   |
| San Francisco.....             | Apr. 28 |           |

The islands visited by the expedition that are known to have endemic species of birds are Guadalupe, the San Benitas, Cedros off Lower California, and Tiburon off the coast of Sonora.

Guadalupe Island, in latitude  $29^{\circ}$  and 135 miles west of San Quintin Bay, is about 20 miles long and from 3 to 7 miles wide. It is mountainous, the greatest height being 4,500 feet. Guadalupe is partly wooded and has a few fresh-water springs. It has been inhabited temporarily.



The following species and subspecies of land birds are peculiar to the island:

*Polyborus lutosus*  
*Colaptes cafer rufipileus*  
*Carpodacus amplus*  
*Junco insularis*

*Pipilo consobrinus*  
*Salpinctes obsoletus guadeloupensis*  
*Thryomanes brevicauda*  
*Regulus calendula obscurus*

There are three small islands in the San Benito group which lie about 15 miles west of Cedros Island. West Benito, the largest island, has a central height of 661 feet. All lack fresh water and are uninhabited. There are two endemic birds, *Passerculus rostratus sanctorum* and *Carpodacus mcgregori*.

Cedros Island, about 10 miles from the nearest point of the mainland, has a length of 21 miles and a width of from 3 to 9 miles. It is mountainous, the highest peak being nearly 4,000 feet. The island is sparsely wooded, with some cedars and pines on the higher elevations. Cedros has a few springs of fresh water and has been temporarily inhabited by miners. The only land bird peculiar to the island is *Thryomanes bewickii cerroensis*.

Tiburon is the largest island in the Gulf; it is thirty miles long by fifteen in width, and has a height of 4,000 feet.

The fauna of Tiburon Island has been derived chiefly from the mainland of Sonora, from which it is separated by a channel varying from one to three miles in width.

None of the thirteen species of land birds secured on Tiburon Island are referable to races belonging to Lower California. The width of the Gulf of California averages considerably greater than that of the peninsula, exceeding 100 miles in the latitude of Guaymas, its central portion. The following land birds were taken on Tiburon Island:

*Passerculus rostratus rostratus*  
*Pipilo fuscus jamesi*  
*Cardinalis cardinalis affinis*  
*Phainopepla nitens*  
*Dryobates scalaris cactophilus*  
*Myiarchus cinerascens cinerascens*  
*Empidonax difficilis difficilis*

*Colaptes chrysoides mearnsi*  
*Centurus uropygialis uropygialis*  
*Toxostoma bendirei*  
*Auriparus flaviceps lamprocephalus*  
*Heleodytes brunneicapillus brunneicapillus*  
*Polioptila plumbea*

One of the birds in the above list (*Pipilo fuscus jamesi*) is described elsewhere in this paper as a new subspecies. It is probable that this large and mountainous island contains other unknown birds. It had not previously been visited by ornithologists. Tiburon is inhabited by Seri Indians believed to be dangerous to small parties. Science as yet knows nothing of the interior of this island.



Although most species of birds should have been nesting at this season, March and April, very few nests were seen.

Birds were collected chiefly by Messrs. H. E. Anthony and P. I. Osburn, although many were obtained by Dr. Paul Bartsch and myself. The naval officers attached to the 'Albatross' brought on board numerous specimens of water birds.

Lower California has not yet been fully explored ornithologically. The following records, relating mostly to the distribution of the species met with, include some localities not previously visited by ornithologists, and are, with a few exceptions, restricted to localities visited by the expedition.



Fig. 1. The 'Albatross' at San Josef Island, Gulf of California.

The nomenclature is that of the A. O. U. list, with such additions as have appeared in Ridgway's 'Birds of North and Middle America.'

For information on the physiography of the localities here referred to, reference may be made to part one of this series of reports, which contains the narrative of the voyage with numerous illustrations.

### ***Colymbus nigricollis californicus* (Heermann)**

#### **EARED GREBE**

The eared grebe was observed at several points in the Gulf, being quite common at San Josef Island, Agua Verde Bay, San Francisquito Bay, and Angel Guardia Island. Eight specimens, San Josef Island, March 30 and San Francisquito Bay, April 10.



***Gavia pacifica* (Lawrence)**

## PACIFIC LOON

One specimen was taken April 11 at Tiburon Island where it was rather abundant. Our notes do not show that it was observed elsewhere.

***Cerorhinca monocerata* (Pallas)**

## RHINOCEROS AUKLET

A single specimen was secured at San Cristobal Bay on March 15. There are no records of this auklet having been found farther south.

***Ptycorhamphus aleuticus* (Pallas)**

## CASSIN'S AUKLET

Four specimens taken: Guadalupe Island, March 2-4, and West. San Benito Island, March 10. We found parts of East Benito so riddled with burrows of auklets that it was difficult to walk without breaking into them. When cruising in the schooner 'Laura' late in November, 1884, I took two specimens of this auklet off San Cristobal Bay.

***Brachyrhamphus craverii* (Salvadori)**

## CRAVERI'S MURRELET

This bird we found only at San Esteban Island in the Gulf, where a single example was secured April 14. San Esteban Island is about twenty miles from Isla Raza where Dr. T. H. Streets found Craveri's murrelet breeding in abundance in April, 1875. The species is peculiar to Lower California and the Gulf regions.

***Larus philadelphia* (Ord)**

## BONAPARTE'S GULL

Specimens were taken at Carmen Island, April 3, Mulege, April 4, and Tiburon Island, April 12. It was fairly common at La Paz on April 18. On March 27, 1889, I obtained this gull in the northern part of the Gulf.

***Larus heermanni* Cassin**

## HEERMAN'S GULL

This species was observed from April 1 to 19 at many points in the Gulf, from Cerralbo Island northward to Angel Guardia and Tiburon islands. It breeds in considerable numbers at Isla Raza and Ildefonso.

***Sterna maxima* Boddaert**

## ROYAL TERN

Numerous at San Josef Island on March 30 and at Guaymas on April 15. Specimens were obtained at San Cristobal Bay, March 15, Abreojos Point, March 16, and Angel Guardia Island, April 10.



***Sterna elegans* Gambel**

## ELEGANT TERN

Common in April at several points in the Gulf from La Paz to Angel Guardia and San Esteban islands. Observed at Guaymas, April 15. Sixteen specimens, one of which was obtained on the west side of the peninsula at Abreojos Point, March 16.

***Puffinus opisthomelas* Coues**

## BLACK-VENTED SHEARWATER

One specimen, San Bartolome Bay, March 13.

***Oceanodroma macrodactyla* W. Bryant**

## GUADALUPE PETREL

Two specimens, Guadalupe Island, March 2-5.

***Oceanodroma kaedingi* Anthony**

## KAEDING'S PETREL

While the 'Albatross' was anchored at Guadalupe Island, March 2-5, nine specimens were captured on board at night, doubtless attracted by the electric lights around the deck house. Petrels were very numerous and their calls were heard about the vessel all night.

***Oceanodroma melania* Bonaparte**

## BLACK PETREL

Two specimens, San Jose del Cabo March 26 and San Francisquito Bay, April 9. On a former voyage I found this petrel abundant off Guaymas.

***Oceanodroma homochroa* (Coues)**

## ASHY PETREL

One specimen, taken on board at night, off San Benito Islands, April 23.

***Sula brewsteri* Goss**

## BREWSTER'S BOOBY

Observed in the Gulf from March 30 to April 18, at most of the points visited by the expedition. One specimen, taken at San Josef Island, March 31. In 1889 I found this booby breeding in considerable numbers at Georges Island near the head of the Gulf.

In 1888 Col. N. S. Goss estimated that about 700 of this species and about 1000 blue-footed boobies were breeding on San Pedro Martir Isle, which lies midway in the Gulf about 25 miles south of Tiburon





Fig. 2. San Pedro Martir Island, Gulf of California.  
Nesting place of *Sula brewsteri*.



Fig. 3. Boobies. U. S. S. 'Albatross,' in the Gulf of California.



Island. At that time a guano company with about 135 employees was removing guano and causing great disturbance among the nesting birds. Col. Goss predicted that with the exhaustion of the guano supply the birds would return in great numbers, and this has evidently taken place. The accompanying photograph taken on April 15 from the deck of the 'Albatross' while passing San Pedro Martir, shows the greater part of the island densely covered with birds. This barren rock, less than a mile in length and width, is over 1000 feet in height. We did not attempt to land, owing to the force of the gale which was blowing.

**Phalacrocorax auritus albociliatus** Ridgway

FARALLON CORMORANT

One specimen, Magdalena Bay, March 20. Cormorants were seen almost daily during the voyage. A compact flock of a thousand or more was seen at Santa Maria Bay, March 18, and a flock of nearly as many at San Roque Island, March 15.

**Fregata aquila** (Linnæus)

MAN-O'-WAR-BIRD

This bird is common about the lower part of the peninsula from Magdalena Bay on the Pacific, where it nests on the mangroves, to Concepcion Bay on the Gulf.

**Chaulelasmus streperus** (Linnæus)

GADWALL

San José del Cabo, March 26, one specimen.

**Marila americana** (Eyton)

REDHEAD

San José del Cabo, March 26, one specimen.

**Anas platyrhynchos** Linnæus

MALLARD

Three mallards were seen at San Josef Island on March 30. Not observed elsewhere.

**Marila affinis** (Eyton)

LESSER SCAUP DUCK

Seen at La Paz and San Josef Island late in March, and at Angel Guardia Island, April 10.



**Nettion carolinense** (Gmelin)

GREEN-WINGED TEAL

A small flock seen at La Paz, March 28.

**Mareca americana** (Gmelin)

BALDPATE

Seen at Angel Guardia Island, April 10. Wild ducks are not common in Lower California as there are few permanent streams and no lakes or fresh-water marshes.

**Oidemia perspicillata** (Linnæus)

SURF SCOTER

A few were observed at Angel Guardia Island, April 10 and 11.

**Mergus serrator** Linnæus

RED-BREASTED MERGANSER

Observed at Mulege, April 4 and at Tiburon Island, April 11.

**Guara alba** (Linnæus)

WHITE IBIS

Rather common at San Josef Island, March 30 to April 1. One specimen.

**Plegadis guarauna** (Linnæus)

WHITE-FACED GLOSSY IBIS

Two specimens, San Jose del Cabo, April 22.

**Botaurus lentiginosus** (Montagu)

AMERICAN BITTERN

Magdalena Bay, March 20, one specimen.

**Ardea herodias treganzai** Court

WESTERN GREAT BLUE HERON

Santa Maria Bay, March 18 and Angel Guardia Island, April 10, two specimens.

**Egretta candidissima** (Gmelin)

SNOWY EGRET

Obtained at San Francisquito Bay, April 9 and at Tiburon Island, April 10.



**Dichromanassa rufescens** (Gmelin)

REDDISH EGRET

Specimens obtained at Magdalena Bay, March 20 and at San Josef Island, March 30. This egret was observed at Concepcion Bay, April 8 and at Guaymas, April 7.

**Hydranassa tricolor ruficollis** (Gosse)

LOUISIANA HERON

Magdalena Bay, March 20, one specimen. Observed at Concepcion Bay, April 7.

**Florida cærulea** (Linnæus)

LITTLE BLUE HERON

Magdalena Bay, March 21, one specimen. Several were seen at La Paz, April 18.

**Butorides virescens frazari** (Brewster)

FRAZAR'S GREEN HERON

Specimens of this form of the green heron were obtained at Santa Maria Bay, March 18, and at San Josef Island, March 31. Green Herons probably of this race were seen at Mulege, April 4.

**Nycticorax nycticorax nævius** (Boddaert)

BLACK-CROWNED NIGHT HERON

Specimens were taken at Abreojos Point, March 16, and at Magdalena Bay, March 22. Night herons apparently of this form were observed at San Josef Island, March 30, and at Concepcion Bay, April 5.

**Nyctanassa violacea** (Linnæus)

YELLOW-CROWNED NIGHT HERON

Taken at Santa Margarita Island, March 20.

**Pisobia minutilla** (Vieillot)

LEAST SANDPIPER

Taken at San Bartolome Bay, March 13 and 14 and at Abreojos Point, March 16.

**Ereunetes mauri** Cabanis

WESTERN SANDPIPER

Obtained at San Bartolome Bay, March 13 and 14, Abreojos Point, March 16, and at Magdalena Bay, March 20.



***Calidris leucophæa* (Pallas)**

SANDERLING

Abreojos Point, March 16, two specimens.

***Limosa fedoa* (Linnæus)**

MARBLED GODWIT

Magdalena Bay, March 20, two specimens.

***Totanus melanoleucus* (Gmelin)**

GREATER YELLOW-LEGS

Abreojos Point, March 16, Magdalena Bay, March 20, five specimens.

***Catoptrophorus semipalmatus* (Gmelin)**

WILLET

Abreojos Point, March 16, five specimens.

***Heteractitis incanus* (Gmelin)**

WANDERING TATLER

Cerro Island, March 10, two specimens.

***Actitis macularis* (Linnæus)**

SPOTTED SANDPIPER

San Bartolome Bay, March 13, Concepcion Bay, April 8, and La Paz, April 9, three specimens.

***Numenius americanus* Bechstein**

LONG-BILLED CURLEW

Abreojos Point, March 16 and Magdalena Bay, March 21, two specimens.

***Numenius hudsonicus* Latham**

HUDSONIAN CURLEW

Santa Margarita Island, March 19, two specimens.

***Squatarola squatarola* (Linnæus)**

BLACK-BELLIED PLOVER

Abreojos Point, March 16, two specimens.

***Oxyechus vociferus* (Linnæus)**

KILLDEER

San Jose del Cabo, March 26 and Miraflores, May 11, three specimens.



***Ægialites semipalmata* (Bonaparte)**

SEMIPALMATED PLOVER

Abreojos Point, March 16, Tiburon Island, April 12, two specimens.

***Ægialitis nivosa* Cassin**

SNOWY PLOVER

Abreojos Point, March 16, Magdalena Bay, March 20, and Carman Island, April 23, eight specimens.

***Ochthodromus wilsonius* (Ord)**

WILSON'S PLOVER

La Paz, March 27, one specimen.

***Aphriza virgata* (Gmelin)**

SURF-BIRD

The surf-bird probably winters in considerable numbers in the Lower California and Gulf region, having been taken at Abreojos Point on the Pacific side of the peninsula on March 16, at San Josef Island in the Gulf on March 31, and at Tiburon Island off the coast of Sonora on April 12. Twenty or more were seen at San Josef Island.

It is not mentioned by Bryant, or Brewster, nor in any of the papers on Lower California birds with which the writer is familiar. Although its migration route extends from Alaska to Chili, it has never been recorded as common anywhere, and its breeding range is still unknown. So far as observed by the writer, it frequents low rocks along shore that are almost a-wash. All that were seen were comparatively fearless, showing little concern when approached.

***Arenaria melanocephala* (Vigors)**

BLACK TURNSTONE

San Roque Island, March 15, Abreojos Point, March 16, and Tiburon Island, April 12, five specimens.

***Hæmatopus frazari* Brewster**

FRAZAR'S OYSTER-CATCHER

San Benito Islands, March 9, Cerros Island, March 10, Magdalena Bay, March 20, San Josef Island, March 31, and San Esteban Island, April 1, seven specimens.

The oyster-catcher was observed at Agua Verde Bay, April 1, Angel Guardia Island, April 10, and Santa Catalina Island, April 16. A nest and eggs were found at Concepcion Bay, April 7.



***Hæmatopus bachmani* Audubon**

## BLACK OYSTER-CATCHER

Cerros Island, March 10, and San Roque Island, March 15, two specimens.

***Lophortyx californica vallicola* (Ridgway)**

## VALLEY QUAIL

Not observed by the expedition on the Pacific coast of the peninsula, but found common at many places on the Gulf coast from Cape San Lucas northward to Agua Verde Bay, seven specimens.

***Columba fasciata vioscæ* Brewster**

## VIOSCA'S PIGEON

Miraflores, April 25, May 5 and 20, and San Bernardo Mountain, May 13, eight specimens. Not seen north of the Cape region.

***Melopelia asiatica mearnsi* Ridgway**

## WESTERN WHITE-WINGED DOVE

Late in March ten specimens were obtained at Cape San Lucas, San Jose del Cabo, and La Paz.

Observed at most points in the Gulf visited by the 'Albatross,' including Tiburon Island.

***Zenaida macroura marginella* (Woodhouse)**

## WESTERN MOURNING DOVE

Cape San Lucas, March 22 and 23. Observed at Mulege, April 4 and at Tiburon Island, April 13.

***Chamæpelina passerina pallescens* Baird**

## MEXICAN GROUND DOVE

Cape San Lucas, March 24, San Jose del Cabo, March 26, six specimens. The ground dove was seen at Mulege, April 4.

***Accipiter cooperi* (Bonaparte)**

## COOPER'S HAWK

Cape San Lucas, March 24, one specimen.

***Parabuteo unicinctus harrisi* (Audubon)**

## HARRIS'S HAWK

Cape San Lucas, March 23, one specimen.



**Buteo borealis calurus** Cassin

WESTERN RED-TAIL

Miraflores, April 25, one specimen.

**Falco sparverius phalæna** (Lesson)

DESERT SPARROW HAWK

West San Benito Island, March 9 and San Jose del Cabo, March 26, three specimens.

**Falco sparverius peninsularis** Mearns

SAN LUCAS SPARROW HAWK

Cape San Lucas, March 24 and Miraflores, May 2 and 18, six specimens.

**Polyborus cheriway** (Jacquin)

AUDUBON'S CARACORA

Santa Margarita Island, March 19 and Magdalena Bay, March 21, two specimens.

**Pandion haliaetus carolinensis** (Gmelin)

OSPREY

Observed at many places. Nests are conspicuous on the uninhabited islands such as Cedros and the San Benitos. Young ospreys were brought on board at Agua Verde Bay.

Cerros Island, March 10, one specimen.

**Asio flammeus** (Pontoppidan)

SHORT-EARED OWL

Cape San Lucas, March 23, one specimen.

**Otus xantusi** Brewster

XANTUS'S SCREECH OWL

Miraflores, April 25 and May 18, twelve specimens.

**Bubo virginianus elachistus** Brewster

DWARF HORNED OWL

Angel Guardia Island, April 11, Espiritu Santo Island, April 18, Miraflores, April 30 and May 12, and La Palma, April 20, eight specimens.



***Speotyto cunicularia hypogeæa* (Bonaparte)**

BURROWING OWL

San Benito Islands, March 9 and Angel Guardia Island, April 10, two specimens.

***Glaucidium hoskinsi* Brewster**

HOSKIN'S PIGMY OWL

Miraflores, April 25 and 30, two specimens.

***Micropallas whitneyi sanfordi* Ridgway**

SANDFORD'S ELF OWL

Miraflores, April 25 and May 11 and San Bernardo Mountain, May 15, eight specimens.

***Geococcyx californianus* (Lesson)**

ROAD RUNNER

A single specimen was taken at San Jose del Cabo, April 24. Although the road runner is an inhabitant of most parts of the peninsula, it was seldom observed by our party. I saw one at San Cristobal Bay, November 16, 1884.

***Megaceryle alcyon* (Linnæus)**

BELTED KINGFISHER

Magdalena Bay, March 20 and La Paz, March 29, two specimens.

***Dryobates scalaris lucasanus* (Xantus)**

SAN LUCAS WOODPECKER

Common from Cape San Lucas to La Paz. Obtained also at Carmen, San Josef, and Santa Cruz islands, 17 specimens.

***Dryobates scalaris cactophilus* Oberholser**

CACTUS WOODPECKER

Tiburon Island, April 12.

***Melanerpes formicivorus angustifrons* Baird**

NARROW-FRONTED WOODPECKER

Miraflores, April 28 and May 8, ten specimens.

***Centurus uropygialis brewsteri* Ridgway**

BREWSTER'S WOODPECKER

Common from Cape San Lucas northward along the Gulf Coast to Mulege, 23 specimens.



**Centurus uropygialis uropygialis** Baird

GILA WOODPECKER

Tiburon Island, April 13, one specimen.

**Colaptes chrysoides chrysoides** Malherbe

GILDED FLICKER

Agua Verde Bay, April 2 and Miraflores, May 17, two specimens.

**Colaptes chrysoides mearnsi** Ridgway

MEARN'S GILDED FLICKER

Tiburon Island, April 13, one specimen.

**Phalænoptilus nuttalli californicus** Ridgway

DUSKY POOR-WILL

Miraflores, May 4, one specimen.

**Chordeiles acutipennis inferior** Oberholser

SAN LUCAS NIGHTHAWK

Miraflores, May 19, one specimen.

**Calypte costæ** (Bourcier)

COSTA'S HUMMING-BIRD

Cerros Island, March 10 and 12, Santa Maria Bay, March 18,  
Agua Verde Bay, April 1, San Josef Island, April 1, ten specimens.

**Calypte anna** (Lesson)

ANNA'S HUMMING-BIRD

Cerros Island, March 12, three specimens.

**Basilinna xantusi** (Lawrence)

XANTUS'S HUMMING-BIRD

San Josef Island, March 31, Agua Verde Bay, April 1, and Mira-  
flores, May 4 and 11, ten specimens.

**Tyrannus vociferans** Swainson

CASSIN'S KINGBIRD

Cape San Lucas, March 23, San Jose del Cabo, March 26. Several  
were seen at Agua Verde Bay, April 2, three specimens.



**Myiarchus cinerascens pertinax** (Baird)

## LOWER CALIFORNIA FLYCATCHER

Common from Cape San Lucas northward along the Gulf coast to San Francisquito Bay. Taken also on San Josef and Cerralbo islands, 33 specimens.

**Myiarchus cinerascens cinerascens** (Lawrence)

## ASH-THROATED FLYCATCHER

Tiburon Island, April 11 and 12, San Esteban Island, April 13 and 14, five specimens.

**Sayornis sayus** (Bonaparte)

## SAY'S PHOEBE

Cerros Island, March 11 and 12 and Cape San Lucas, March 24.

**Empidonax difficilis cineritius** Brewster

## SAN LUCAS FLYCATCHER

San Josef Island, March 31 and Agua Verde Bay, April 2.

**Empidonax difficilis difficilis** Baird

## WESTERN FLYCATCHER

Tiburon Island, April 12.

**Empidonax trailli trailli** (Audubon)

## TRAILL'S FLYCATCHER

San Bernardo Mountain, May 15. The only specimen secured is tentatively referred to the western form.

**Empidonax wrighti** Baird

## WRIGHT'S FLYCATCHER

Cape San Lucas, March 23 and 24, La Paz, March 30, and Santa Cruz Island, April 16, seven specimens.

**Otocoris alpestris actia** Oberholser

## CALIFORNIA HORNED LARK

Cerros Island, March 10, San Bartolome Bay, March 13 and 14. Shore larks were seen at Carmen Island, April 3.

**Aphelocoma californica hypoleuca** Ridgway

## XANTUS'S JAY

Found from Santa Maria Bay on the Pacific to Concepcion Bay on the Gulf coast, 18 specimens.



**Corvus corax sinuatus** Wagler

RAVEN

Specimens were taken at Cerros Island, March 12, Abreojos Point, March 16, and San Bartolome Bay, March 14. Ravens were seen at nearly all points visited by the expedition including Tiburon Island.

**Icterus parisorum** Bonaparte

SCOTT'S ORIOLE

Cape San Lucas, March 23 and 24, Miraflores, April 25 and May 6. Seen also at Tiburon Island, April 11.

**Icterus cucullatus nelsoni** Ridgway

ARIZONA HOODED ORIOLE

Common from Cape San Lucas northward along the Gulf coast to Agua Verde Bay. Seen also at Carmen Island, 11 specimens.

**Carpodacus mexicanus ruberrimus** Ridgway

SAN LUCAS HOUSE FINCH

Common from Miraflores northward to Mulege. Observed also at Espiritu Santo and Santa Catalina islands, 29 specimens.

**Carpodacus mexicanus clementis** Mearns

SAN CLEMENTE HOUSE FINCH

Cerros Island, March 12.

**Carpodacus mexicanus frontalis** (Say)

HOUSE FINCH

The house finches seen on Tiburon and San Esteban islands were probably of this form, which occurs in Sonora.

**Carpodacus amplus** Ridgway

GUADALUPE HOUSE FINCH

Guadalupe Island, March 1, 28 specimens.

**Carpodacus mcgregori** Anthony

MCGREGOR'S HOUSE FINCH

West San Benito Island, March 9.

**Astragalinus psaltria hesperophilis** Oberholser

GREEN-BACKED GOLDFINCH

San Jose del Cabo, March 25, Agua Verde Bay, April 2, and Mulege, April 4.



***Passerculus sandwichensis alaudinus* Bonaparte**

WESTERN SAVANNAH SPARROW

San Bartolome Bay, March 13.

***Passerculus rostratus guttatus* Lawrence**

SAN LUCAS SPARROW

Abreojos Point, March 16, Santa Maria Bay, March 19, and Magdalena Bay, March 20 and 21, ten specimens.

***Passerculus rostratus rostratus* (Cassin)**

LARGE-BILLED SPARROW

Found at most points on the peninsula visited by the expedition and also at Tiburon Island, 16 specimens.

***Passerculus rostratus sanctorum* Ridgway**

SAN BENITO SPARROW

San Benito Island, March 9, 16 specimens.

***Chondestes grammacus strigatus* Swainson**

WESTERN LARK SPARROW

Cape San Lucas, March 22 and 24, five specimens.

***Zonotrichia leucophrys leucophrys* (J. R. Forster)**

WHITE-CROWNED SPARROW

San Bartolome Bay, March 13, Cape San Lucas, March 24, and San Jose del Cabo, March 26.

***Zonotrichia coronata* (Pallas)**

GOLDEN-CROWNED SPARROW

Cerro Island, March 12 and Cape San Lucas, March 24.

***Spizella pallida* (Swainson)**

CLAY-COLORED SPARROW

Cape San Lucas, March 24, five specimens.

***Spizella breweri* Cassin**

BREWER'S SPARROW

Cape San Lucas, March 24, Carmen Island, April 3, and Espiritu Santo Island, April 19, five specimens.

***Junco insularis* Ridgway**

GUADALUPE JUNCO

Guadalupe Island, March 2, five specimens.



**Amphispiza bilineata deserticola** Ridgway

DESERT SPARROW

Taken at nearly all points visited by the expedition including San Esteban, Carmen, Santa Catalina, Santa Cruz, and Espiritu Santo islands.

**Melospiza lincolni lincolni** (Audubon)

LINCOLN'S SPARROW

Tiburon Island, April 12.

**Pipilo maculatus magnirostris** Brewster

LARGE-BILLED TOWHEE

San Bernardo Mountain, May 14.

**Pipilo fuscus albigula** Baird

SAN LUCAS TOWHEE

San Bernardo Mountain, May 10, Miraflores, May 7-10.

**Pipilo fuscus jamesi**, new subspecies

TIBURON ISLAND TOWHEE

SUBSPECIFIC CHARACTERS.—Smaller than *P. f. intermedius*, but bill and feet larger; coloration similar but paler throughout; chin, throat, breast and abdomen paler; upper parts and flanks much more ashy, ear coverts slightly ashier; anal and femoral regions and under tail-coverts decidedly less tawny; crown lighter rufous.

Aver. of 2 ♀.—Length (skin), 198. Wing, 88. Tail, 92. Culmen, 15. Tarsus, 24. Middle-toe, 25.

Aver. of 2 ♂.—Length (skin), 197. Wing, 90. Tail, 89. Culmen, 16. Tarsus, 23. Middle-toe, 24.

TYPE.—No. 131,854, Amer. Mus. Nat. Hist., ♂ ad., Tiburon Island.

In general appearance of under parts this bird has more resemblance to *P. f. albigula*, the Lower California form, than to *intermedius* of the adjacent Sonoran mainland, but is paler than either. The Tiburon birds were compared with specimens from Guaymas, taken March 3 to 23. Tiburon Island, April 12, 13. 4 specimens.

Named for Mr. Arthur Curtiss James of New York.

**Oreospiza chlorura** (J. K. Townsend)

GREEN-TAILED TOWHEE

Specimens were taken at Cape San Lucas, March 24 and La Paz, March 29. It was observed also at Tiburon Island.



***Cardinalis cardinalis igneus* Baird**

## SAN LUCAS CARDINAL

Found by the expedition in the Cape region where it is common and as far north as Concepcion Bay. Specimens were taken also at Carmen Island.

***Cardinalis cardinalis affinis* Nelson**

## ALAMOS CARDINAL

The single specimen of this genus, a female, secured at Tiburon Island on April 12 is tentatively referred to *affinis*, but appears to be smaller with larger feet.

***Pyrrhuloxia sinuata peninsulæ* Ridgway**

## SAN LUCAS PYRRHULOXIA

This bird was found by our party only at the extreme lower end of the peninsula, being taken at Cape San Lucas on March 23 and 24 and at San Jose del Cabo on March 26, seven specimens.

***Zamelodia melanocephala* (Swainson)**

## BLACK-HEADED GROSBEAK

Cape San Lucas, March 24, Agua Verde Bay, April 12, Concepcion Bay, April 2, and Miraflores, May 10, six specimens.

***Passerina amoena* (Say)**

## LAZULI BUNTING

Concepcion Bay, April 7. Observed at San Francisquito Bay, April 9, and at Tiburon Island, April 13.

***Passerina versicolor pulchra* Ridgway**

## BEAUTIFUL BUNTING

Miraflores, May 7 and 17, San Bernardo Mountain, May 14, six specimens.

***Calamospiza melanocorys* Stejneger**

## LARK BUNTING

Cerros Island, March 11, Santa Margarita Island, March 20, and Cape San Lucas, March 23, seven specimens.

The record for Cerros Island indicates an extension of its known range. It was observed at Carmen and Tiburon islands.



**Tachycineta thalassina brachyptera** Brewster

SAN LUCAS SWALLOW

San Jose del Cabo, March 25 and 26, Agua Verde Bay, April 2, San Francisquito Bay, April 9, Espiritu Santo Island, April 18, 13 specimens.

**Phainopepla nitens** (Swainson)

PHAINOPEPLA

Obtained at Agua Verde Bay, April 1 and 2, Tiburon Island, April 12, and Miraflores, May 7, 11 specimens.

Although known to be common in many parts of the peninsula, we did not see it except at the points mentioned.

**Lanius ludovicianus gambeli** Ridgway

CALIFORNIA SHRIKE

Shrikes were taken at Cape San Lucas, March 24, San Jose del Cabo, March 25, and Angel Guardia Island, April 11. They were observed also at Tiburon Island.

**Vireosylva gilva swainsoni** (Baird)

WESTERN WARBLING VIREO

Miraflores, April 25 and May 17 and San Bernardo Mountains, May 13, seven specimens.

**Lanivireo solitarius lucasanus** (Brewster)

SAN LUCAS VIREO

Same localities and dates as preceding, eight specimens.

**Vireo belli pusillus** Coues

LEAST VIREO

Santa Cruz Island, April 16.

**Vermivora celata lutescens** (Ridgway)

LUTESCENT WARBLER

Santa Margarita Island, March 17 and 18 and Cape San Lucas, March 23.

**Dendroica bryanti castaneiceps** Ridgway

MANGROVE WARBLER

Santa Maria Bay, March 17 and 18, La Paz, March 27, and San Jose del Cabo, March 25, six specimens.

This warbler is common among the mangroves at Santa Maria Bay.



***Dendroica auduboni auduboni* (J. K. Townsend)**

AUDUBON'S WARBLER

Cerros Island, March 12, and at sea, north of Guadalupe Island, April 25.

***Dendroica nigrescens* (J. K. Townsend)**

BLACK-THROATED GRAY WARBLER

Concepcion Bay, April 8.

***Seiurus noveboracensis notabilis* Ridgway**

GRINNELL'S WATER THRUSH

Magdalena Bay, March 21.

***Geothlypis trichas arizela* Oberholser**

PACIFIC YELLOW-THROAT

Magdalena Bay, March 20 and 21.

***Geothlypis beldingi* Ridgway**

BELDING'S YELLOW-THROAT

San Jose del Cabo, March 24 and 25 and Miraflores, May 5 and 9, six specimens.

***Wilsonia pusilla pileolata* (Pallas)**

PILEOLATED WARBLER

At sea, north of Guadalupe Island, April 25.

***Anthus rubescens* (Tunstall)**

AMERICAN PIPIT

San Jose del Cabo, March 26 and Carmen Island, April 3.

***Oreoscoptes montanus* (J. K. Townsend)**

SAGE THRASHER

San Bartolome Bay, March 13, four specimens.

***Mimus polyglottos leucopterus* (Vigors)**

WESTERN MOCKINGBIRD

Specimens were taken at Cerros Island, March 11, Magdalena Bay, March 19, Cape San Lucas, March 23 and 24, La Paz, March 27 and 30, and at Aguá Verde Bay, April 2.

The mockingbird was observed also at Mulege, Concepcion Bay, San Francisquito Bay, and Tiburon Island. It was fairly common wherever met with.



**Toxostoma bendirei** (Coues)

BENDIRE'S THRASHER

Tiburon Island, April 3.

**Toxostoma cinereum cinereum** (Xantus)

SAN LUCAS THRASHER

Cape San Lucas, March 23, San Jose del Cabo, March 25, Agua Verde Bay, April 1 and 2, and Miraflores, May 9 and 10.

**Heleodytes brunneicapillus affinis** (Xantus)

SAN LUCAS CACTUS WREN

Cape San Lucas, March 23, San Jose del Cabo, March 25 and 26, La Paz, March 29 and April 19, Agua Verde Bay, April 1 and 2, and Miraflores, May 19.

**Heleodytes brunneicapillus brunneicapillus** (Lafresnaye)

GUAYMAS CACTUS WREN

Tiburon Island, April 12.

**Salpinctes obsoletus obsoletus** (Say)

ROCK WREN

San Benito Islands, March 9 and Magdalena Bay, March 21.

**Salpinctes obsoletus guadeloupensis** Ridgway

GUADALUPE ROCK WREN

Guadalupe Island, March 2, ten specimens.

**Catherpes mexicanus polioptilus** Oberholser

INTERMEDIATE CANYON WREN

Espiritu Santo Island, April 18 and 19.

**Thryomanes bewickii cerroensis** (Anthony)

CERROS ISLAND WREN

Cerro Island, March 12, three specimens.

**Telmatodytes palustris plesius** (Oberholser)

WESTERN MARSH WREN

San Francisquito Bay, April 10.

**Auriparus flaviceps lamprocephalus** Oberholser

CAPE VERDIN

Magdalena Bay, March 19 and 21, Cape San Lucas, March 23 and 24, La Paz, March 30, Agua Verde Bay, April 2, Concepcion Bay, April



6 and 7, Angel Guardia Island, April 11, Cerralbo Island, April 19, Miraflores, May 10 and 11, and Tiburon Island, April 12.

A nest and two eggs were taken at Cape San Lucas on March 23, and a nest with three eggs at Tiburon Island, April 12, the eggs on the latter date being at the point of hatching.

***Polioptila cærulea obscura* Ridgway**

WESTERN GNATCATCHER

Specimens were taken at La Paz, March 29 and 30, Agua Verde Bay, April 12, Concepcion Bay, April 9, Cerralbo Island, April 19, Miraflores, May 8.

It was observed also at Mulege and Santa Catalina Island, and was rather common at most of the localities where it was found.

***Polioptila plumbea* (Baird)**

PLUMBEOUS GNATCATCHER

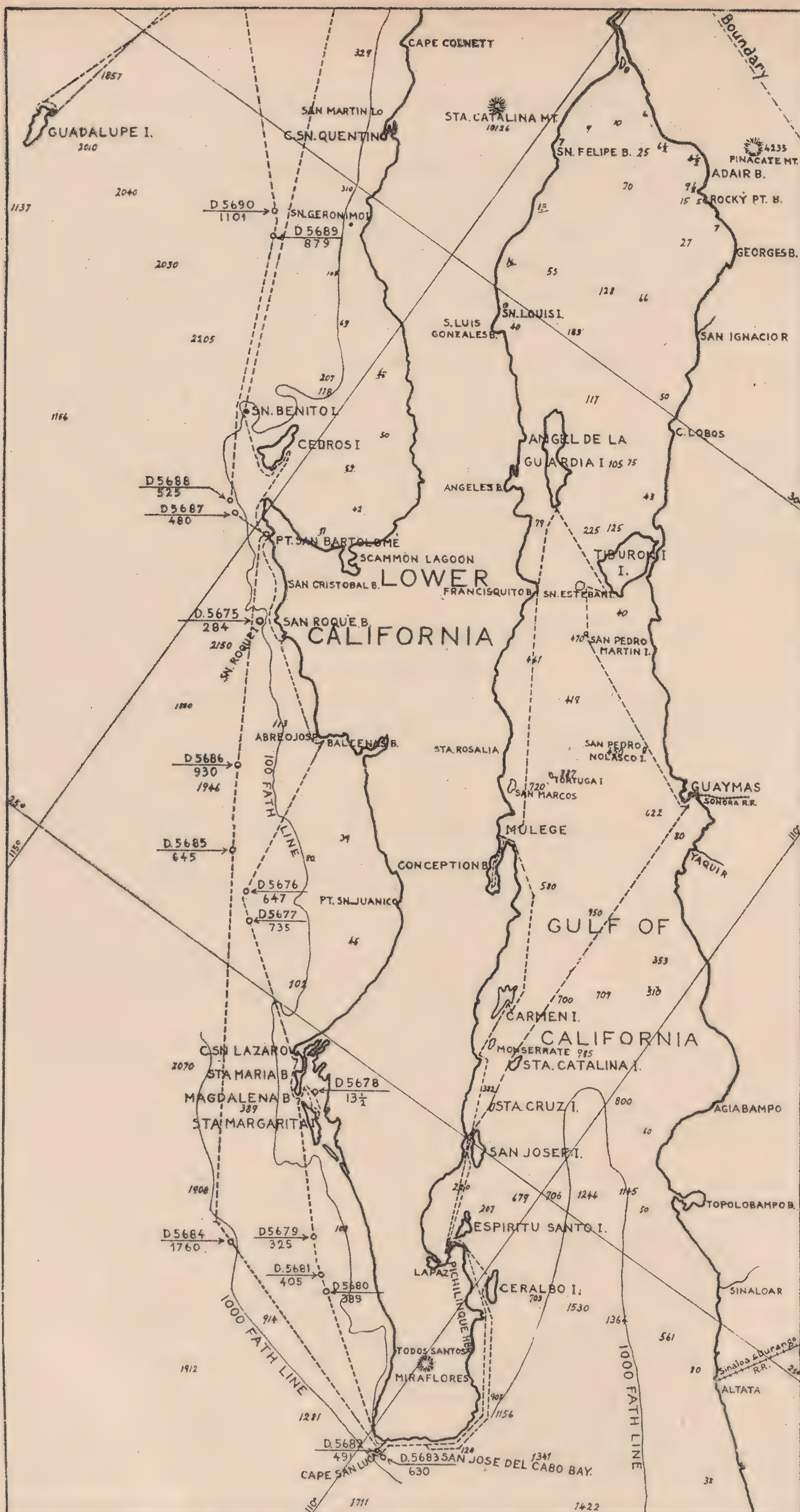
Santa Margarito Island, March 19, Cape San Lucas, March 24, San Jose del Cabo, March 26, La Paz, March 29 and 30, and Tiburon Island, April 12.

***Planesticus confinis* (Baird)**

SAN LUCAS ROBIN

San Bernardo Mountain, May 12-15, three specimens.





MAP OF THE LOWER CALIFORNIA REGION  
SHOWING ROUTE OF THE ALBATROSS EXPEDITION IN 1911  
UNDER THE DIRECTION OF C.H. TOWNSEND



## Article II.—THE DISTRIBUTION OF THE MOTMOTS OF THE GENUS *MOMOTUS*

BY FRANK M. CHAPMAN

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### INTRODUCTION

The motmots, a distinctively American family of birds, range from the northern limit of the Tropical Zone in northeastern Mexico south to the southern limit of this zone in northern Argentina. The family contains six genera,<sup>1</sup> approximately fifteen species, and some twenty-two subspecies.

All six genera are represented in Central America but, barring the occurrence of *Hylomanes* in northwestern Colombia, only three are present in South America.

Of the fifteen-odd species contained in the family, three are common to South America and Central America, four are exclusively South American, and eight are exclusively Central American. Thus both in genera and species the motmots are more numerously represented in Middle than in South America.

Motmots are sedentary, tree-inhabiting birds. The rufous-crowned species of the genus *Momotus* inhabit semi-arid regions where cacti and mimosas are characteristic growths. The blue and black-and-blue-crowned species of this genus haunt deep forests but are by no means

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<sup>1</sup>I see no generic distinction between *Baryphthengus* and "*Urospatha*." On the contrary, both agree and differ from all other members of the group in possessing greatly enlarged auricular tufts, while their pectoral tufts are disproportionately small. Our specimens show no constant difference in tomial serration nor in relative length of tarsus to middle-toe, while east of the Andes "*Urospatha*" *martii* agrees with *Baryphthengus* in having the central rectrices normally non-spatulate.



restricted to heavily wooded areas. Scrubby growth and "gallery" forests bordering streams afford them sufficient cover, a fact which no doubt in a large measure accounts for their wide distribution.

They nest in holes in banks or similar places and lay white eggs, their nidification resembling, therefore, that of their relatives the todies and kingfishers.

In this paper I attempt to show that the motmots originated in Middle America; that they have made at least three invasions of South America, of which the last two have occurred since the elevation of the Andes; that the earlier of these post-Andean invasions was made by a Subtropical Zone bridge over Panama, which has since disappeared; and that the second originated in the Tropical Zone of Panama with a subsequent center of dispersal east of the Andes in Colombia. In order fully to present the facts on which these conclusions rest it will be necessary to review the species of the genus concerned.

#### THE GENUS *MOMOTUS*

The range of the genus *Momotus* is nearly coëxtensive with that of the family to which it belongs. Its members fall into two distinct groups, in one of which the crown is cinnamon-rufous or chestnut, in the other blue, or black and blue. No two forms of either group are found associated and, in spite of their distinctness, even the rufous-crowned and black-and-blue-crowned species are not known to occur together. Dr. E. W. Nelson, who has had wide field experience in Mexico, writes me in response to my request: "Not one of our many field records shows both of these species from the same locality. We have many records of each of these but always from distinct places, so that the evidence appears to be against their ranges overlapping, unless it may be a very narrow territory along the borders."

#### THE RUFOUS-CROWNED GROUP

On the Pacific slope of Mexico and in Guatemala two species of motmots with reddish-brown heads are found. They are

*Momotus mexicanus mexicanus* Swains.

*Momotus mexicanus saturatus* Nels.

*Momotus castaneiceps* Gould.

*Momotus mexicanus mexicanus* is found, according to Ridgway, in the states of Sinaloa, Tepic, Durango, Zacatecas, Jalisco, Colima, Michoacan, Mexico, and Puebla; and it is also recorded from Vera Cruz on the authority of Sumichrast, but examination of the page



cited in the work of that author<sup>1</sup> reveals only a reference to "*Momotus lessoni*," the east Mexican species.

*Momotus mexicanus saturatus* Nels., a closely related, larger race having the brown of the head suffusing the back, represents *mexicanus* in the states of Guerrero, Oaxaca, and Chiapas.

These two birds bear no close relationship to the blue-and-black-crowned group which forms the special subject of this paper, but it is worthy of note that, in spite of their unlikeness, the two are apparently never found associated.

*Momotus castaneiceps* of Guatemala, though evidently representing *mexicanus*, is specifically distinct from it. Its distribution is given by Salvin and Godman as the "Valley of the Motagua river between the narrow gorge near Guastatoya and La Magdalena, and the denser forest which commences above Gualan. This includes the whole of the plain of Zacapa, which is comparatively open country, large cacti and mimosa trees being the characteristic plants."<sup>2</sup>

#### THE BLUE OR BLACK-AND-BLUE-CROWNED GROUP

Our inquiry lies with the blue or black-and-blue, rather than rufous-crowned, species, and the latter are mentioned to show that the southern Mexico-Guatemala<sup>3</sup> region appears to have been a point of origin and subsequent dispersal of two distinct groups of the genus *Momotus*, one of which, in Mexico, is restricted to the Pacific, the other to the Atlantic side; and that in spite of their wide divergence no two species are found associated, and that consequently they bear to each other the relationship of representative species.

In this section of the genus *Momotus* are included the following species and subspecies. I begin with the most northern species and proceed, generally, southward.

|                                          |                                                  |
|------------------------------------------|--------------------------------------------------|
| <i>Momotus caeruliceps</i>               | Eastern Mexico.                                  |
| <i>Momotus lessoni goldmani</i>          | Southeastern Mexico.                             |
| "        " <i>exiguus</i>                | Peninsula of Yucatan.                            |
| "        " <i>lessoni</i>                | Central America to Subtropical Zone in Chiriqui. |
| <i>Momotus æquatorialis æquatorialis</i> | Subtropical Zone, Colombia; Ecuador.             |
| <i>Momotus æquatorialis chlorolæmus</i>  | Subtropical Zone, Peru.                          |
| <i>Momotus subrufescens conexus</i>      | Magdalena Valley north to Canal Zone.            |
| <i>Momotus subrufescens reconditus</i>   | Eastern Panama, Atrato Valley.                   |

<sup>1</sup>1869, Mem. Bost. Soc. Nat. Hist., p. 560.

<sup>2</sup>Biol. Cen. Amer. Aves, II, p. 461.

<sup>3</sup>In this connection the restriction of the genus *Aspatha* to the highlands of Guatemala doubtless possesses some significance.



|                                          |                                                              |
|------------------------------------------|--------------------------------------------------------------|
| <i>Momotus subrufescens subrufescens</i> | Northern Colombia; northern Venezuela.                       |
| <i>Momotus subrufescens osgoodi</i>      | Southern Maracaibo region.                                   |
| <i>Momotus bahamensis</i>                | Trinidad; Tobago.                                            |
| <i>Momotus momota microstephanus</i>     | Eastern Colombia; eastern Ecuador.                           |
| <i>Momotus momota momota</i>             | Between Orinoco and Amazon.                                  |
| <i>Momotus momota argenticinctus</i>     | Western Ecuador.                                             |
| <i>Momotus momota ignobilis</i>          | Eastern Peru.                                                |
| <i>Momotus momota nattereri</i>          | Bolivia.                                                     |
| <i>Momotus momota pilcomajensis</i>      | Southern Bolivia; N. W. Argentina; southern Brazil.          |
| <i>Momotus momota simplex</i>            | Right side, Lower Amazon, to Santarem; south central Brazil. |
| <i>Momotus momota parensis</i>           | Pará region east of Tocantins.                               |
| <i>Momotus momota cametensis</i>         | Lower Amazon, west of Tocantins.                             |

From this list it appears that of the some thirty-seven species and subspecies contained in the family Momotidæ more than one-half are contained in the black-and-blue-crowned section of the genus *Momotus*.

Although six of the twenty forms included in this section are ranked as species, no two are found associated. In other words, the various members of the group replace one another in their respective ranges, extending from near the Rio Grande Valley at the north southward to northern Argentina. While in some instances the non-intergradation of a form with its geographic neighbor or neighbors establishes what we term its specific distinctness, it seems evident that, viewed in the broader biologic rather than the narrower taxonomic sense, we have here one widely, almost continuously, distributed, plastic type represented by twenty forms exhibiting various degrees of differentiation. In short, the blue-and-black-crowned group of the genus *Momotus* is apparently now the dominant, most highly developed type of the family.

Before attempting to determine what light the relationships and distribution of these birds may throw on evolutionary and faunal problems, it will be necessary briefly to review their characters, status, and ranges.

The peculiar plumage of motmots occasions the systematist some difficulty in defining their true colors. Seen directly from above, the upperparts of some species appear to be green; viewed at an angle, especially toward the light, the same part is rich brown. Occasionally, however, individuals of one species from the same locality may be either green or brown without regard to the angle from which they are viewed, and species showing this extreme of variation might well be considered dichromatic in color.



It was obviously variation of this kind which led to the description, for example, of *Momotus bartletti*, and the systematist requires, therefore, adequate series of specimens to ascertain the prevailing type of color in a given form.

#### THE MIDDLE AMERICAN FORMS AND THEIR ANDEAN REPRESENTATIVE

The motmots of Mexico and Central America have been treated by Ridgway<sup>1</sup> so recently that the appended summary of their range and relationships is based chiefly on his work. The conclusions therein presented are supported by a study of our own large series except in the case of *Momotus cæruliceps*, the intergradation of which with *lessoni* is indicated by our material. Since, however, the recognition of such intergradation would involve ranking all the Middle American forms as subspecies of *cæruliceps*, it seems inadvisable to make this nomenclatural change until intergradation of *cæruliceps* with *lessoni* is proven.

#### ***Momotus cæruliceps* (Gould)**

*Prionites cæruliceps* GOULD, 1836, Proc. Zool. Soc., p. 18 (Tamaulipas, Mexico).

CHARACTERS.—Resembling *M. l. goldmani* but pileum wholly blue, forehead tinged with greenish; underparts less tawny; breast-tuft larger.

RANGE.—Tropical Zone of northeastern Mexico from Nuevo Leon south to the state of Vera Cruz.

Ridgway includes Córdoba, Vera Cruz, and Rinconada, Puebla, in the range of this species, but does not state whether the Córdoba record is based on actual examination of specimens. We have a skin of *goldmani* from Monte de Cuichapa, Córdoba, with the crown strongly washed with blue of exactly the same shade as in *cæruliceps*, while the general color of the body is decidedly greener than in a specimen of *cæruliceps* from Valles, San Luis Potosi. In the latter the greenish frontal area is less pronounced than in true *cæruliceps*, but if it were accepted as typical of *cæruliceps*, the Córdovan specimen would certainly be referred to that species rather than to *lessoni goldmani*.

#### ***Momotus lessoni goldmani* Nelson**

*Momotus lessoni goldmani* NELSON, 1900, Auk, XVII, p. 256 (Motzorongo, Vera Cruz, Mex.).

CHARACTERS.—Differs from *M. lessoni lessoni* of Central America in being greener, in having the breast much less strongly tinged with brown, and particularly in the absence of cobalt-blue in the posterior blue margin to the black pileum. The black margin to the nuchal band appears to be more evident in this race.

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<sup>1</sup>1914, Bull. U. S. Nat. Mus., VI, pp. 450-487.



RANGE.—Humid Tropical Zone of southeastern Mexico from the southern limits of the range of *M. cæruliceps* south to Tabasco.

Though much nearer *lessoni*, the characters which separate *goldmani* from *lessoni* mark it as an intermediate between that form and *cæruliceps*. The typical form, with no cobalt-blue in the blue nuchal band, occurs only at the northern limit of the range assigned to the race, and is obviously an approach toward *cæruliceps*.



Fig. 1. Distribution of *Momotus lessoni* Group.

- |                                 |                                |
|---------------------------------|--------------------------------|
| 1. <i>M. cæruliceps</i> .       | 4. <i>M. lessoni lessoni</i> . |
| 2. <i>M. lessoni goldmani</i> . | 5. <i>M. æquatorialis</i> .    |
| 3. <i>M. lessoni exiguus</i> .  |                                |

Note the absence of the group from Panama and its extension southward in the Subtropical Zone.

### ***Momotus lessoni exiguus* Ridgway**

*Momotus lessonii exiguus* RIDGWAY, 1912, Proc. Biol. Soc. Wash., XXV, p. 89 (Temax, Yucatan).

CHARACTERS.—Averaging greener than *M. l. goldmani* but agreeing with it and differing from *M. l. lessoni* in having much less or no tawny on the breast; agreeing



with *lessoni* and differing from *goldmani* in having the cerulean blue nuchal band margined posteriorly with smalt-blue.

RANGE.—Tropical eastern Campeche and Yucatan.

While in some respects this form is an intermediate between *lessoni* and *goldmani* in its lighter green color, it differs from them both.

Although traces of smalt-blue are found in the nuchal band of most specimens of *goldmani* from the southern limit of the range of that form, we now encounter this marking for the first time as a constant character and will find it present in variable degrees in all the remaining forms of the group.

### ***Momotus lessoni lessoni* Lesson**

*Momotus lessonii* LESSON, 1842, Rev. Zool., p. 174 (Realejo, Nic.).

CHARACTERS.—Foreback and nape suffused with tawny, occasionally traces of chestnut-rufous in the nape; breast with a pronounced tawny wash, throat greenish blue; posterior pileum usually cerulean tipped with smalt-blue, the longer underlying feathers black.

RANGE.—Tropical to Subtropical Zone, from extreme southern Mexico south to Costa Rica and Chiriqui.

This species at the South and *M. caeruliceps* at the North mark respectively the extremes of differentiation of the Middle American forms of this group. Their intergradation as the range of one form passes into that of another is proven in the case of all of them except *caeruliceps* and with that form it is strongly indicated.

*Momotus caeruliceps* and *Momotus lessoni goldmani* are apparently confined to the Tropical Zone. Sumichrast<sup>1</sup> includes the last-named among the species which characterize the "Hot Region" of Vera Cruz, but from Guatemala southward *lessoni* has a wider altitudinal range.

In Guatemala, Dearborn<sup>2</sup> states that *lessoni* was common on the Pacific slope or San José (sea-level), Mazatenango and Patulul (each 1800 feet). Salvin,<sup>3</sup> however, mentions it as a bird of the "high region."

Of the distribution of *lessoni* in Costa Rica, Carriker writes that it is found throughout the plateau region and the Pacific slope from Nicaragua to Chiriqui. In Chiriqui, Brown records it only from near Boquete at altitudes of from 2500 to 4000 feet.

It appears, therefore, that, whereas in southern Mexico *lessoni* is confined to the Tropical Zone, in Costa Rica and Chiriqui, if not confined to, it is at least characteristic of the Subtropical Zone.

<sup>1</sup>1869, Mem. Bost. Soc. N. H., I, p. 560.

<sup>2</sup>1907, Field Mus. Pub. 125, p. 89.

<sup>3</sup>1860, Ibis, p. 100.



Chiriqui marks the southern known limit of this species. From Chiriqui to the Canal Zone so little collecting has been done that we do not know what form of motmot inhabits this region. So far as our information goes, therefore, the group next appears in the Canal Zone, where we first encounter *Momotus subrufescens*, which is evidently specifically distinct from *M. lessoni*.

***Momotus æquatorialis æquatorialis* Gould**

*Momotus æquatorialis* GOULD, 1857, Proc. Zool. Soc., p. 223 (Archidona, E. Ecuador).

*Momotus lessoni gualeæ* LÖNNBERG AND RENDAHL, 1922, Arkiv für Zool., Band XIV, No. 25, p. 51 (Gualea, Ec.).

CHARACTERS.—Most nearly resembling *Momotus lessoni goldmani* but larger, the tawny suffusion of the breast extending to the abdomen, the throat averaging less greenish blue; the blue border to the pileum wider, its black margin above the nape more pronounced; under wing-coverts and wing-lining with no trace of cinnamon. Immature birds have more blue on the crown, the black patch being much reduced and in one female (Salento, Col., September 26, 1911) it is practically wanting, the entire crown being blue.

RANGE.—Subtropical Zone of all three ranges of the Colombian Andes, and of the eastern slope of the Andes in Ecuador. (Unknown from western Ecuador?)

*Momotus æquatorialis* is clearly the representative in the Andean Subtropical Zone of the Middle American *M. lessoni*. That it should more closely resemble the Mexican, rather than the geographically nearer Costa Rican form of that species is doubtless due to that type of parallelism which makes *subrufescens* of the Caribbean coast nearest to *simplex* of southern Brazil, and *pilcomajensis* of southern Bolivia almost identical with *argenticinctus* of western Ecuador.

The discovery that a representative of *lessoni* is found in the Andean Subtropical Zone adds another species to the list of between sixty and seventy birds of which the same or obviously representative forms are found in this zone in Costa Rica and in Chiriqui, and in eastern Panama and northwestern Colombia, but are unknown in the low, intervening, tropical area. This subject is discussed in my 'Distribution of Bird-Life in Colombia' (p. 151) and the bearing of the present case on the distribution of the genus *Momotus* in South America will be returned to later.<sup>1</sup>

<sup>1</sup>Since writing the above, I find that Hellmayr (1911, Proc. Zool. Soc., p. 1194) has already suggested the possibility of *æquatorialis* being a southern form of *lessoni*, and Lönnberg and Rendahl (*loc. cit.*) have described a specimen, said to have been taken below Gualea, in western Ecuador, as *Momotus lessoni gualeæ*. It seems, however, doubtful if the specimen in question actually came from Gualea. During a visit to Quito in August, 1922, I showed the leading native collectors specimens of *Momotus æquatorialis* and they assured me that this species had never been found by them in western Ecuador. Mr. Ludovic Söderstrom, whose guest I was while in Quito, tells me he is now convinced that the specimen of *Momotus æquatorialis* which he sent to Dr. Lönnberg, and which is the type of *gualeæ*, must have been erroneously labelled. In any event, the characters ascribed to this proposed race are shown by a series from Colombia to be apparently individual rather than geographic.



***Momotus æquatorialis chlorolæmus* Berlepsch and Stolzmann**

*Momotus æquatorialis chlorolæmus* BERLEPSCH AND STOLZMANN, 1902, Proc. Zoöl. Soc., p. 35 (Ocobamba, N. W. of Cuzco, Peru).

CHARACTERS.—Similar to *M. æ. æquatorialis* but underparts biscay-green with little or no tawny suffusion; throat more greenish blue.

RANGE.—Subtropical Zone of eastern Peru south at least to Santo Domingo.

This form is separated on average differences, a specimen from Santo Domingo being essentially like one from Rio Toché, Colombia. Three other specimens, however, are greener below than any I have seen from Colombia.

## THE SOUTH AMERICAN TROPICAL FORMS

***Momotus subrufescens conexus* Thayer and Bangs**

*Momotus conexus* THAYER AND BANGS, 1906, Bull. Mus. Comp. Zoöl., p. 215 (Sabana de Panama; topotypes examined).

CHARACTERS.—An intermediate between *M. subrufescens subrufescens* and *M. s. reconditus*; underparts more nearly resembling, but somewhat darker than in the former; upperparts more like those of the latter, but not quite so dark; blue of the head as in *reconditus*.

RANGE.—Cauca-Magdalena Fauna in Colombia, northwest, probably on the Caribbean coast region of Panama, at least to the Canal Zone and Savannah of Panama, and doubtless westward toward Chiriqui.

In my 'Distribution of Bird-Life in Colombia' (p. 271) I referred the motmots of the Magdalena Valley to *subrufescens subrufescens*. A broader view of their relationships shows, in my opinion, that, while specimens from the lower, more arid part of the valley are indeed referable to *subrufescens*, those from the more humid central portion of the valley are intermediate between that race and the deeply colored *reconditus*; while those from the semi-arid extreme upper Magdalena Valley are not quite so deeply colored as those from the more heavily forested part of the valley. Considered as a whole, these upper Magdalena birds are not unlike Canal Zone specimens, as Ridgway has already remarked.<sup>1</sup> In other words, they more nearly agree with the form known as *conexus* than with *subrufescens*. So far, therefore, as Colombia is concerned, the three forms of *subrufescens* may each be assigned to an existing faunal area as follows: (1) *M. s. subrufescens*, Caribbean Fauna; (2) *M. s. conexus*, Cauca-Magdalena Fauna; (3) *M. s. reconditus*, northern part of Colombian-Pacific Fauna. Whether the Colombian range of *conexus* is connected with the area this form occupies in Panama, I do not know. No such connection evidently exists on the Pacific side of the Caribbean costal

<sup>1</sup>Bull. U. S. Nat. Mus., L, part 6, p. 462.



range, for this region is inhabited by *reconditus*. Possibly, however, *conexus* may be found on the Caribbean side of this range, though one would imagine that the heavy rainfall that characterizes this region would produce as deeply colored a form as that which exists in the Tuyra and Atrato Valleys.



Fig. 2. Distribution of the *Momotus subrufescens* Group.

- |                                             |                                               |
|---------------------------------------------|-----------------------------------------------|
| 1. <i>Momotus subrufescens conexus</i> .    | 3. <i>Momotus subrufescens subrufescens</i> . |
| 2. <i>Momotus subrufescens reconditus</i> . | 4. <i>Momotus subrufescens osgoodi</i> .      |
|                                             | 5. <i>Momotus bahamensis</i> .                |

Confined to northern Colombia, the coastal region of Venezuela, Trinidad and Tobago. The form of the lower Orinoco is quite unlike that of Trinidad and northeast Venezuela.

We should, however, regard these variations in color as expressions of environment, chiefly if not wholly climatic, under which the individuals exhibiting them exist.

Considered thus from a biological, rather than nomenclatural, standpoint we have a species, *Momotus subrufescens*, ranging from at least the Canal Zone in Panama to the islands of Trinidad and Tobago. Being apparently continuously distributed throughout this region, it



encounters a wide range of climatic conditions from the semi-arid coastal region of Colombia and Venezuela to the humid districts of the Tuyra, Atrato, upper Magdalena, southern Maracaibo basin and islands of Trinidad and Tobago. In the drier parts of its range this motmot is comparatively light colored (*subrufescens subrufescens*); in the moister areas it is more richly colored (*conexus*, *reconditus*, *osgoodi*, and *bahamensis*).

It is of special importance to note that, although northeastern Venezuela is the only place, under existing topographic conditions, where *Momotus* could cross the Andean system without leaving the Tropical Zone, the forms found on the Caribbean slope and in Trinidad are less closely related to *M. m. momota*, the form of the lower Orinoco and the Guianas, the nearest one to them geographically, than to any other one in the group. Whether or not the ranges of *subrufescens* and *momota* come together I do not know, but the available evidence assuredly does not point to their intergradation.

Trinidad forms are usually closely related to those of the lower Orinocan and Guianan region, but in this case it seems quite clear that the Trinidad form has been derived from the Caribbean coast region of Venezuela rather than from the south, and we have further support here, therefore, for our belief that the distribution of *Momotus* has been from the north southward.

#### ***Momotus subrufescens reconditus* (Nelson)**

*Momotus conexus reconditus* NELSON, 1912, Smiths. Misc. Coll., p. 27 (Marragante, E. Panama; type examined).

CHARACTERS.—More richly colored than *M. s. subrufescens*, the underparts nearly, if not quite, as deep as in *M. bahamensis*, but the throat and breast with a greenish caste; upperparts much darker than in *M. s. subrufescens*, parrot-green, suffused with tawny; cerulean blue of the crown deeper.

RANGE.—Eastern Panama and Valley of the Atrato in Colombia.

The rich colors of this well-marked race express the influence of the exceptionally humid region it inhabits. No species of this group has been found in western Colombia south of the Atrato, and it is especially noteworthy that the form of western Ecuador differs widely from that of northern Colombia.

#### ***Momotus subrufescens subrufescens* Sclater**

*Momotus subrufescens* SCLATER, 1853, Rev. et Mag. de Zool., V, p. 489 (Santa Marta, Col. Topotypes examined).

*Momotus venezuelæ* SHARPE, 1892, 'Cat. Birds, Brit. Mus.,' XVII, p. 321 (prov. description of "Venezuelan specimens"; no type mentioned; specimens from San Esteban and Puerto Cabello listed).



CHARACTERS.—Underparts rufous-tawny, greener anteriorly, more rufous posteriorly; upperparts varying from parrot-green washed with olivaceous to rufous-tawny nearly as deep as in the underparts of some specimens, but usually with a pronounced tawny suffusion, at least anteriorly, and usually with more or less concealed chestnut on the nape. Differs from *lessoni* in its smaller size, more slender bill, rufous-tawny underparts and more tawny back; tawny instead of greenish or greenish-tawny lower wing-coverts, more cerulean blue of forehead, absence of black margin to the nuchal band, and concealed chestnut on the nape.

RANGE.—Caribbean coastal region of Colombia and Venezuela.

The status and relationship of this race are discussed under *M. s. conexus*. Specimens from northern Venezuela are apparently not separable from true *subrufescens*.

Among forms inhabiting the interior of South America, *subrufescens* is nearest *simplex* of South Central Brazil, from which it differs chiefly in its more tawny upperparts.

#### ***Momotus subrufescens osgoodi* Cory**

*Momotus osgoodi* CORY, 1913, Field Mus. Pub. 167, p. 285 (El Guayabel, 10 m. east of Cúcuta, Colombia).

CHARACTERS.—Upperparts suffused with tawny as in true *subrufescens*, but much darker; underparts uniform chestnut-rufous as in *bahamensis*.

RANGE.—Humid forests of the southern half of the Gulf of Maracaibo.

Again responding to a more humid environment *Momotus subrufescens* becomes much deeper in color both above and below. Six of the seven specimens examined are indistinguishable below from *bahamensis*, but above are suffused with tawny; the seventh, which has a tinge of greenish on the throat and is greener above, can be closely matched by a specimen of *reconditus* from eastern Panama.

#### ***Momotus bahamensis* (Swainson)**

*Prionites bahamensis* SWAINSON, 1837, 'Anim. in Menag.,' p. 332 (Trinidad; topotypes examined).

CHARACTERS.—Underparts from bill to vent uniform rich hazel or chestnut-rufous; no green on the throat; upperparts darker green, with much less brownish suffusion than in *subrufescens*; tawny on nape often wanting.

RANGE.—Islands of Trinidad and Tobago.

An island representative of *subrufescens* which, evidently through complete isolation, has become specifically distinct. There is no apparent difference between Trinidad and Tobago specimens.

In spite of the close resemblance usually found among Trinidad, lower Orinocan, and Guianan species, it is noteworthy that *bahamensis* is an evident derivative of the Caribbean coastal form, and differs from *momota momota* more than from any other race in the group.



We now leave the *subrufescens* group, cross the Andes, and find an apparently specifically distinct but representative group in the various races of *Momotus momota*.

***Momotus momota microstephanus* Sclater**

*Momotus microstephanus* SCLATER, 1855, Proc. Zool. Soc., p. 135 ("Interior of New Grenada" = region about Villavicencio, east of Bogotá; type examined; a "Bogotá" skin).

CHARACTERS.—Prevailing color of underparts greenish when viewed from above, but decidedly medal bronze when seen at a slight angle or on a level with the eye, and this bronze becomes more tawny when the bird is held between the observer and the light; the nuchal band is broadly smalt-blue with little or no cerulean, the chestnut-rufous border more pronounced, as a rule, than in any other form except *momota*; central rectrices of adults not always spatulated; general tone of back much as in *conexus*.

RANGE.—Colombia (and Ecuador?) east of the Andes.

The only species of *Momotus* definitely known to occur in the "interior" of Colombia (that is, west of the Eastern Andes) are *M. subrufescens* (including its races) and *M. æquatorialis*. Specimens from the Bogotá region on the Rio Meta, east of Villavicencio, agree with the type of *microstephanus*, and are doubtless topotypes of it. While they average slightly greener above than specimens from southeastern Colombia, the two series certainly represent but one form. In a former paper<sup>1</sup> I referred the latter to *M. m. ignobilis*, but the receipt of specimens of this race from the Perené near La Merced, Peru, whence Berlepsch and Stolzmann record typical examples of *ignobilis*, shows conclusively that I was in error. The difference between the two is not, however, so great that it might not be bridged by the range of individual variation and to this fact I attribute the record<sup>2</sup> of *ignobilis* based on an immature specimen from "Mataben, Rio Orinoco," a place I am unable definitely to locate.

The Colombian birds are intermediate between *momota* and *ignobilis* but are nearer to the former in color and to the latter in size. A specimen from Florencia, southeastern Colombia, has more chestnut-rufous on the nape than one from Cayenne. It is also significant that of eight adult specimens of *microstephanus* only four have the central rectrices spatulate, a fact which indicates their close relationship to *momota*, of which only two in twelve adults in our collection have racquet-tipped rectrices. In short, in view of the fact that the ranges of *microstephanus* and *momota* are doubtless connected, there is every reason to believe that the birds themselves intergrade.

<sup>1</sup>1917, Bull. Amer. Mus. Nat. Hist., XXXVI, p. 271.

<sup>2</sup>1902, Berlepsch and Hartert, Nov. Zool., p. 106.



To the south there is equally good reason to believe that *microstephanus* intergrades with *ignobilis*, while in western Ecuador it is surprising to find it subspecifically represented by *argenticinctus*.



Fig. 3. Distribution of *Momotus momota* Group.

- |                                           |                                          |
|-------------------------------------------|------------------------------------------|
| 1. <i>Momotus momota microstephanus</i> . | 5. <i>Momotus momota pilcomajensis</i> . |
| 2. " " <i>momota</i> .                    | 6. " " <i>simplex</i> .                  |
| 3. " " <i>ignobilis</i> .                 | 7. " " <i>cametensis</i> .               |
| 4. " " <i>nattereri</i> .                 | 8. " " <i>parensis</i> .                 |
| 9. <i>Momotus momota argenticinctus</i> . |                                          |

Note that only the Ecuador form, No. 9, is found west of the Andes. Although apparently derived from No. 1 it most closely resembles No. 5. Although the ranges of Nos. 6, 7, and 8 are separated from that of No. 2 only by the Amazon, the differences between the first three and the last are apparently of specific value, but all are indirectly connected through Nos. 3 and 1.

### ***Momotus momota momota* (Linnæus)**

*Ramphastos momota*, LINNÆUS, 1766, 'Syst. Nat.,' p. 152 (Cayenne; topotype examined).

CHARACTERS.—Largest form of the group; central rectrices usually non-spatulate; a large chestnut-rufous post-nuchal band or spot sharply defined from the back, which averages purer green than in *microstephanus*; wing-lining and under wing-coverts with less cinnamon than in *microstephanus*; crown and its border as in that race; underparts yellowish green.



RANGE.—Region between the Orinoco, Rio Negro and Amazon; westward doubtless in Colombia to the district in which it probably intergrades with *microstephanus*, eastward to the Atlantic.

The name of this form, the first race described, has of necessity to be employed as the specific designation of the forms of the group with which directly or indirectly it intergrades.

This race has close relationships only with *microstephanus*, with which, as has been said, it probably intergrades in eastern Colombia.

It is important to observe that to the north its range approaches that of the quite different *subrufescens* and insular *bahamensis*, while on the south the Amazon separates it at Obidos from the quite unlike *simplex* of Santarem. In discussing the relationship of the last-named form, I have given my reasons for the belief that *parensis* and *cametensis* were derived from it rather than direct from true *momota*.

#### The East Ecuador Form

Unfortunately I have no specimens from eastern Ecuador. Doubtless, however, the bird of that region is between *microstephanus* and *ignobilis* and, in view of the characters shown by specimens from southeastern Colombia, it is probable the east Ecuador bird is nearer the former. Whether or not it shows any approach toward the west Ecuador form remains to be determined. Berlepsch (Journ. für Orn., 1889, p. 307), in describing *ignobilis*, refers east Ecuador specimens to it. But he also remarks that La Merced specimens agree with his *ignobilis*. Sharpe describes a bird from the upper Ucayali as *bartletti* and refers Colombian specimens (= *microstephanus*) to it. These facts indicate the close resemblance between northeast Peruvian and east Colombian birds, and lead to the conclusion that the east Ecuadorian bird is *microstephanus*.

#### ***Momotus momota argenticinctus* Sharpe**

*Momotus argenticinctus* SHARPE, 1892, 'Cat. Birds Brit. Mus.,' XX, p. 323, prov. (Babahoyo, Ec.; type examined).

CHARACTERS.—Nearest to *M. m. microstephanus* but anterior underparts averaging greener, the throat usually tinged with bluish green, much as in *lessoni*, the posterior pileum band usually with more cerulean, less smalt-blue; nuchal region greener less suffused with tawny; rectrices always spatulate in the adult.

RANGE.—Tropical Zone of western Ecuador and northwestern Peru from Esmeraldas to Palambla.

This paper originated in an attempt to determine the affinities of the form of *Momotus* inhabiting Ecuador, and its extent is an indication of the length to which such attempts of necessity sometimes lead one.



It was important, in the first place, to ascertain what races of this group were found in the Tropical Zone of Colombia, where it appears that only *subrufescens subrufescens* and *subrufescens reconditus* are known. Neither of these birds is closely related to *argenticinctus*; and *reconditus*, of the Atrato Valley, the nearest to it geographically, is the least like it of the two. South of the valley of the Atrato no form of *Momotus* has been found in western Colombia; but whether or not one occurs it is not conceivable that *reconditus* intergrades with *argenticinctus* in this area. We must therefore look elsewhere for the ancestor of the west Ecuador bird and we find it, I think, in *microstephanus* of eastern Colombia and (doubtless) eastern Ecuador.

I am not unmindful of certain characters which *argenticinctus* shares with *lessoni*, but the latter is so obviously represented in South America by *æquatorialis* that it is not to be considered as the ancestor of *argenticinctus*. Furthermore, the differences between the last-named form and *microstephanus* are practically bridged by individual variation and in spite, therefore, of their disconnected ranges, I list them as subspecifically related.

#### ***Momotus momota ignobilis* Berlepsch**

*Momotus brasiliensis ignobilis* BERLEPSCH, 1889, Journ. für Orn., p. 307 (Yurimaguas, Peru).

*Momotus bartletti* SHARPE, 1892, 'Cat. Birds Brit. Mus.,' XVIII, p. 321, Pl. x (Upper Ucayali).

CHARACTERS.—Described by Berlepsch as smaller than *momota* with less, or without, chestnut-rufous on the nape and with the underparts greener.

Three specimens from the Perené, near La Merced (whence Berlepsch and Stolzmann record *ignobilis*) agree with this description in part but have the abdomen distinctly more rufescent than in *momota* and in this respect agree with Sharpe's description of "*bartletti*." They have not, however, the amount of chestnut on the nape which he ascribes to that species. Sharpe refers a "Bogotá" specimen to his "*bartletti*" but none of our Colombian birds matches the three very uniformly colored Perené specimens in the greenness of their breast and quite strongly contrasted cinnamon abdomen. The Perené birds further differ from *microstephanus* in the practical absence of cerulean in the post-pileum band and of rufescent suffusion on the foreback. Two of them have, however, a trace of chestnut-rufous in the nape.

In the color of the underparts the Perené birds can be exactly matched by one from Todos Santos, Rio Chaparé, Bolivia, but above they are purer green than any of our Bolivian specimens; and in this



respect resemble *simplex*, with which the Peruvian bird doubtless merges. A large series from Chapada, Matto Grosso, includes specimens which are almost identical with the Perené birds, though the latter are less rufescent on the abdomen than the average Chapada examples.

It is clear that with only three east Peruvian birds at hand, and those not topotypical of the bird recognized from that region, I am not in a position satisfactorily and definitely to discuss the relationships of the birds of this area. But it is also equally clear from these birds, and the descriptions of other authors, that *microstephanus* of eastern Colombia and *nattereri* of Bolivia are connected by specimens from the intervening area, but just what part of this area may be allotted to the form known as *ignobilis* I am unable to say.

#### ***Momotus momota nattereri* Sclater**

*Momotus nattereri* SCLATER, 1857, Proc. Zoöl. Soc., p. 251 (Yungas, Bolivia; topotypical specimens examined).

*M[omotus] boliviana* REICHENOW, 1919, Journ. für Orn., p. 335 (La Paz, Bolivia).

CHARACTERS.—Underparts (seen from above) uniform rich rufescent olive, the abdominal region not, as a rule, strikingly different from the breast and never as deep cinnamon-rufous as in *simplex*; breast more rufescent than in Perené specimens of *ignobilis*; upperparts dark and more suffused with tawny than in *ignobilis*, *simplex*, or *pilcomajensis*.

RANGE.—Tropical Zone at the northeastern base of the Bolivian Andes, doubtless merging with *simplex* toward the east and *ignobilis* toward the north.

The range of *nattereri* has hitherto been applied to all Brazilian specimens south of the Amazon, except those of the Pará region, but it is evident that this name cannot properly be applied to birds from Santarem, and Matto Grosso specimens prove to be nearer to the Santarem than to the Yungas form. Evidently, therefore, the name *nattereri* should be restricted to Bolivian birds. This question is dealt with further under *simplex*.

#### ***Momotus momota pilcomajensis* Reichenow**

*Momotus pilcomajensis* REICHENOW, 1919, Journ. für Orn., p. 334 (Villa Monte, Rio Pilcomayo, S. Bolivia).

CHARACTERS.—Greener below than *M. m. nattereri*, with less, or only a tinge of, cinnamon on the abdomen; the throat bluish green; the upperparts green as in *simplex*; differing from *M. m. argenticinctus* only in the absence of a cerulean margin at the back of the pileum.

RANGE.—Southern Bolivia, northern Argentina, and eastward to Urucum and possibly western São Paulo, Brazil.

Two specimens (one from Vermejo, 3500 ft., Dept. Santa Cruz, Bolivia; the other from Urucum, near Corumbá, Brazil) agree with the description of this form, the most southern of the genus. They agree



minutely in general coloration with average specimens of *argenticinctus* of western Ecuador, even to the greenish blue throat, but the Vermejo bird has the post-pileum band almost wholly smalt-blue with only a trace of cerulean at the bases of some feathers, while in the Urucum bird the cerulean is more evident. The latter and a bird from Santa Rosa, Ecuador, are as nearly alike as two birds can well be.

We have here, therefore, an even more pronounced case of parallelism than is shown by *simplex* and *subrufescens*.

### **Momotus momota simplex**, new subspecies

SUBSPECIFIC CHARACTERS.—Underparts much as in *M. s. subrufescens* but back much purer green (grass-green) without tawny suffusion, except to a limited degree anteriorly, where, in some individuals, there is a trace of chestnut-rufous; abdominal region more rufescent than in *nattereri*, the cinnamon-rufous extending, in most specimens, to the throat, back purer green, size larger; closely resembling *M. m. parensis* but with no or but little chestnut-rufous on the nape.

TYPE.—No. 73,372, Carnegie Museum, ♂ ad. Santarem, Brazil, June 30, 1919; S. M. Klages.

RANGE.—Right bank of the Amazon, from at least the Tapajoz westward probably to near the Peruvian boundary; southward to the head of Amazonian drainage in Matto Grosso, and probably Goyaz.

Specimens from the range ascribed to this race have hitherto been identified as *nattereri*, but in loaning me an excellent series in the Carnegie Museum, from Santarem, Mr. Todd calls my attention to the characters which distinguish the Amazonian from the Bolivian bird. Prior to the receipt of these birds, I had described a large series from Chapada, Matto Grosso, as "greener above and more rufescent below than totypical Bolivian birds," adding "these characters are most pronounced in two specimens from Santarem."

Until further specimens were received from Santarem, I did not feel convinced of the desirability of separating the Brazilian birds. However, comparison with Bolivian specimens now shows this course to be apparently unavoidable, and the preceding diagnosis is presented with Mr. Todd's kind permission.

To the Santarem form I would refer our Matto Grosso series, as nearer to *simplex* than to true *nattereri*. Specimens from Goyaz should doubtless also be placed with *simplex*, but since a bird from Urucum on Paraguayan drainage agrees with one from Vermejo, Bolivia, which I have identified as *pilcomajensis*, I am uncertain whether a record by von Ihering from Itapura on Paraguayan drainage, in western São Paulo, should be placed under *simplex* or *pilcomajensis*.



In the comparatively pure green color of the upperparts, *simplex* resembles the three specimens from the Rio Perené in the Chanchamayo district of Peru, and it is more than probable that the Amazonian form is a derivative of the Peruvian, rather than of the Bolivian bird.

From *parensis*, *simplex* differs only in being slightly less rufous on the throat, and in having little or no chestnut-rufous on the nape. In other words, *parensis* has the rufous of the underparts as much, or more highly developed than in any other form south of the Amazon. In this respect, therefore, it differs more widely from *momota momota*, which has greenish underparts, than from any other race of this group. In the amount of chestnut-rufous on the nape, on the other hand, it is nearer *momota momota*.

This character, however, is a variable one, even in *momota momota*, and, in my opinion, is of less importance in determining true affinities than is the color of the underparts. Furthermore, *parensis*, so far as my material and the records go, always has the central rectrices in the adult spatulate, while in true *momota* they are usually untrimmed. I feel, therefore, that the relationships of *parensis* are with *simplex* rather than with *momota momota*, and that the Amazon has been an effective barrier to the distribution of *momota momota* south of its left bank.

In this connection, however, we must consider the form from the left bank of the Tocantins described by Dr. Snethlage as *Momotus momota cametensis* (see beyond). Although occurring between the ranges of *simplex* and *parensis*, with no obvious physical or climatic barrier to prevent continuity of range and consequent intergradation, *cametensis* is said to differ from *parensis* in having the chestnut nuchal band of that form extended to the ear-coverts. Thus this geographically intermediate form is less like *simplex* than the latter is like *parensis*.

It should also be observed that in *cametensis* the chestnut-rufous band is even more developed than in *momota momota*. In the intensity of the rufous below, however, it agrees with *simplex* and *parensis* and, as said above, I consider this character of more significance than that of the nuchal band.

Viewed more broadly, it seems evident that we have south of the Amazon one plastic species of motmot which reflects the influences of a widely varying environment chiefly through the amount of cinnamon-rufous in its plumage, mainly of the underparts.

#### ***Momotus momota cametensis* Snethlage**

*Momota momota cametensis* SNETHLAGE, 1912, Orn. Monatsb., XX, p. 155 (Cameta, left bank of the Rio Tocantins).

CHARACTERS.—Described as similar to *M. m. parensis* but with the chestnut-rufous nuchal band extending to the black ear-coverts.



Unfortunately I have seen no specimens of this race, which Dr. Snethlage states is based on five specimens. Its status is briefly commented on under the preceding form.

### **Momotus momota parensis Sharpe**

*Momotus parensis* SHARPE, 1892, 'Cat. Birds Brit. Mus.,' XVII, p. 320; prov. descr. (Pará, Brazil).

CHARACTERS.—Underparts rich cinnamon-rufous, much as in *subrufescens subrufescens*, but throat without green; closely resembling *M. m. simplex* in general coloration both above and below, but chestnut-rufous nuchal band much as in *momota momota*; differs from that race in being smaller, cinnamon-rufous instead of greenish below, and in having the central rectrices spatulate in the adult.

RANGE.—Pará region east of the Tocantins, to the Parnahyba in the state of Maranhão, Brazil.

The relationships of this form are discussed under *M. m. simplex*.

#### LIST OF SPECIMENS EXAMINED<sup>1</sup>

*Momotus mexicanus mexicanus*.—MEXICO, Sinaloa: Manzanillo Bay, 1 ♂; Escuinapa, 1 ♀; Sierra de Armigas, 3500 ft., 1 ♂, 1 ♀; Los Pielos, 3500 ft., 2 ♂; Nayarit; Tepic, 3 ♂; Amatlan de Canas, 2 ♂, 3 ♀; Jalisco; Tuxpan, 2 ♂, 2 ♀; La Pisagua, 1 ♂, 1 ♀; La Laja, 1 ♂; Sal se Puede, 1 ♀; Wakenakili Mts., 3 ♀; Volcan de Nieve, 1 ♀; Colima; Plains Colima, 1 ♂, 2 ♀.

*Momotus mexicanus saturatus*.—MEXICO, Oaxaca: Tehuantepec, 3 ♂, 3 ♀; Rincon Antonio, 1 ♂.

*Momotus caeruliceps*.—MEXICO, Nuevo Leon: Soto la Marina, 1 ♀; Tamaulipas: Rio Corona, 1; Victoria, 2 ♂, 2 ♀; Xicotencatl, 1 ♂, 2 ♀; Alta Mira, 1 ♀; Jimenez, 1 ♀; Rio Palone, 1 ♀; San Fernando, 1 ♂; Tampico, 1 ♂.

*Momotus lessoni goldmani*.—MEXICO: Monte de Cuichapa, 1 ♀; Rio de Givicia, Oaxaca, 800 ft., 1 ♂; Tolosa, 3 ♂, 2 ♀; Chimalapa, Tehuantepec, 3 ♂.

*Momotus lessoni exiguus*.—YUCATAN: 1 ♂.

*Momotus lessoni lessoni*.—GUATEMALA: 1 ♂, 1; Central Guatemala (Coban to Clusec), 1. HONDURAS: 1. NICARAGUA: Matagalpa, 3 ♂; Chinandega, 2700 ft., 2 ♂, 3 ♀; Las Sabalos, San Juan River, 1 ♂. COSTA RICA: 1; Heredia, 1; San José, 1 ♀. PANAMA: Boqueron, Chiriqui, 5 ♂, 6 ♀, 1; Chiriqui, 1 ♂, 3; Boquete, Chiriqui, 1 ♂, 1 ♀.

*Momotus æquatorialis æquatorialis*.—COLOMBIA: La Florida, Cauca, 6600 ft., 2 ♂, 1 ♀; Los Tambos, 1 ♂, 1 ♀; Rio Lima, 2 ♂; Salento, 7000 ft., 2 ♀; La Tigre, 7500 ft., 1 ♂, 1 ♀; above Salento, 9000 ft., 1 ♀; Rio Toché, 6800 ft., 1 ♂, 1 ♀; Sta. Elena, Antioquia, 9000 ft., 1 ♂; El Roble, 7200 ft., 1 ♀; Andalucia, 5000 ft., 1 ♀; Andalucia, 7000 ft., 1 ♀; "Bogotá:" 1. "ECUADOR:" 1; near Baeza, 1 ♂.

<sup>1</sup>I am indebted to Mr. W. E. Clyde Todd, of the Carnegie Museum, for the loan of 12 specimens of *Momotus momota simplex* from Santarem and vicinity, and for a specimen of *M. m. microstephanus* from Palmar, Colombia, and for 4 specimens of *M. m. parensis* from Pará; to Dr. C. W. Richmond, of the National Museum, for 2 specimens of *parensis* from Pará, and to Dr. W. H. Osgood, of the Field Museum, for 7 specimens of *osgoodi* from the Maracaibo region. The remaining specimens here listed are in The American Museum of Natural History.



*Momotus æquatorialis chlorolæmus*.—PERU: Tulumayo, 4000 ft., 1 ♀; Santo Domingo, 6000 ft., 1 ♂, 1 ♀; Oconeque, 1 ♂.

*Momotus subrufescens conexus*.—PANAMA: Canal Zone, 1 ♂, 1 ♀. COLOMBIA: Puerto Berrio, 1 ♀; Malena, 1 ♂, 1 ♀; Honda, 1 ♂, 2 ♀; Chicoral, 1.

*Momotus subrufescens reconditus*.—EASTERN PANAMA: Boca de Cupe, Tuyra River, Darien, 2 ♂; Cituro, Cupe River, Darien, 1 ♂; Chepigana, 2 ♂. COLOMBIA: Atrato River, Chocó, 1 ♂; River Salaqui, Chocó, 1 ♂.

*Momotus subrufescens subrufescens*.—COLOMBIA: Sta. Marta, 3?; Bonda, 5 ♂, 1 ♀, 16?; La Playa, near Barranquilla, 1 ♂; Magdalena River, 50–100 ft., 19. VENEZUELA: Barquisimeto, Estado Lara, 2 ♂, 1 ♀; El Cuji, Estado Lara, 1 ♂.

*Momotus subrufescens osgoodi*.—COLOMBIA: near Cúcuta, 1 ♂ (type), 1 ♀. VENEZUELA: Orope, 3 ♂, 2 ♀.

*Momotus bahamensis*.—TRINIDAD: 3 ♂, 2 ♀, 1? TOBAGO, B. W. I.: 2 ♂, 3 ♀, 3?

*Momotus momota microstephanus*.—COLOMBIA: "Bogotá," 4?; Palmar, Boyaca, 1 ♀; Villavicencio, base E. Andes, 1600 ft., 2 ♂; Barrigon, head of Rio Meta, 1 ♀; La Morelia (R. Bodoquera), Caquetá, 600 ft., 1 ♂, 1 ♀; Florencia, Caquetá, 675 ft., 2 ♀.

*Momotus microstephanus argenticinctus*.—ECUADOR: Esmeraldas, 4 ♀, 1 ♂; Chone, Manaví, 2 ♂, 3 ♀; Naranjo, Prov. Guayas, 1 ♂, 2 ♀; Rio Pindo, Prov. del Oro, 1850 ft., 1 ♂, 1 ♀; Santa Rosa, Prov. del Oro, 2 ♂; Portovelo, Prov. del Oro, 2000–2700 ft., 1 ♂, 1 ♀; Salvias, Rio Salvias, Zaruma-Zaraguro Trail, 3600 ft., 1 ♂, 1 ♀. PERU: Paletillas, Prov. Piura, 1550 ft., 3 ♂, 1 ♀.

*Momotus momota momota*.—VENEZUELA: Boca de Sina, Cunucunuma River, Upper Orinoco, 440 ft., 2 ♂, 3 ♀; Foot of Mount Duida, Upper Orinoco, 700 ft., 2 ♂; Suapure, 1 ♂, 1 ♀; La Union, Caura, 2 ♂. BRITISH GUIANA: Wismar, Demarara River, 100 ft., 1 ♂. FRENCH GUIANA: Cayenne, 1?

*Momotus momota ignobilis*.—PERU: Perené, Prov. Junin, 2000 ft., 2 ♂, 1 ♀.

*Momotus momota nattereri*.—BOLIVIA: Reyes, 1?, Lower Beni, 1; Mission San Antonio, Rio Chimoré, 1300 ft., 1 ♂; Todos Santos, Rio Chaparé, 1300 ft., 1 ♀, 1 ♂.

*Momotus momota pilcomajensis*.—BOLIVIA: Vermejo, Prov. Santa Cruz, 3,500 ft., 1 ♂. BRAZIL: Urucum, near Corumbá, Matto Grosso, 1 ♂.

*Momotus momota simplex*.—BRAZIL: Santarem, 3 ♂ (inc. type), 7 ♀, 2? Villa Braza, Tapajos, 1 ♀; Miritituba, Tapajos, 1 ♀; Matto Grosso, Chapada, 12 ♂, 9 ♀.

*Momotus momota parensis*.—BRAZIL: Pará, 2 ♂, 2 ♀, 2?

## CONCLUSIONS

### GEOGRAPHIC ORIGIN OF THE MOTMOTS

It appears from the preceding review that the motmots are more numerous represented, both in genera and in species, in Middle than in South America, that the more primitive types of the family (*Aspatha* and *Hylomanes*) are practically restricted to that area, and that certain South American forms have been derived from Middle American ancestors. Furthermore, it may be added that the Todidæ, the only family of birds peculiar to the West Indies, find their nearest known relatives in the early momotine genus *Hylomanes* of Middle America.<sup>1</sup>

<sup>1</sup>In this connection see Murie, 1872, *Ibis*, p. 394; Miller, 1915, *Bull. Amer. Mus. Nat. Hist.*, XXXIV, p. 139.



These facts indicate that the motmots originated in Middle America. I am aware that the reasons here given for the belief that the motmots were dispersed from Middle America are not in accord with Matthew's<sup>1</sup> views that the most primitive members of a group are not found at its center of dispersal but at the periphery of its range. The more generalized motmots (genus *Momotus*) of South America are, however, clearly of northern origin. This statement applies not only to the numerous and evidently recently evolved forms of the Tropical Zone, but particularly to *Momotus æquatorialis* of the Subtropical Zone in the Andes of Colombia, Ecuador, and Peru. In accordance with the law that all forms of the life zones above the basal Tropical Zone must have originated in a lower zone, we find the ancestral form of *æquatorialis* in the Tropical Zone of southern Mexico. In this instance range extension from what I assume to be the present center of dispersal seems proven.

When to this recent evidence we add the proof of the antiquity of the group in Middle America as evinced by the relationships of the West Indian Todidæ to the Middle American primitive and momotine genus *Hylomanes*, it seems to me that the known facts in the case all support the belief that Middle America is the present center of dispersal of the motmots.

The development in Middle America of the strongly marked generic types which are now found associated there implies the former existence of conditions affording the isolation favorable to such development. Possibly this may have occurred in that period (Oligocene, according to Scott, 'History of Land Mammals,' p. 117) when Middle America was broken into a series of islands.

#### THE CASE OF *Baryphthengus*

It is true that an isolated species of motmot, *Baryphthengus ruficapillus*, occurs in southeastern Brazil, a region in which we look for ancestral types. But, as I have attempted to show, this bird is generically like "*Urospatha*" *martii*, a species found from Nicaragua southward. It is a far less primitive type than the Middle American genera *Hylomanes* and *Aspatha*, indeed is closely related to the dominant genus *Momotus*. It seems, therefore, more logical to conclude that *Baryphthengus* has been derived from the north than that the northern forms were derived from *Baryphthengus*.

More than a thousand miles now separate the ranges of *Baryphthengus ruficapillus* from that of *B. martii*. A similar hiatus exists in the

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<sup>1</sup>1915, 'Climate and Evolution,' Ann. N. Y. Acad. Sci., XXIV, p. 180.



Fig. 4. Distribution of *Baryphthengus*.

1. *B. martii semirufa*.
2. *B. martii martii*.
3. *B. ruficapilla*.

Note the absence of this genus from Venezuela, the proximity of the ranges of *semirufa* and *martii* near the head of the Magdalena, and the wide area separating the range of *martii* from that of *ruficapilla*. The range of *Electron* is essentially like that of *Baryphthengus* excluding that of *B. ruficapilla*.

range of other forms which are represented in the southeastern Brazilian region, but are not again encountered until the Andean region is reached (e.g., *Pyroderus*, *Scytalopus*).

The discovery of marine deposits of Tertiary age in the upper Amazon is, of course, incontrovertible evidence of the existence of an "Amazonian Sea."

Haseman,<sup>1</sup> however, arguing for the reversal of the Amazon, states that this sea is of Pacific not Atlantic origin and hence we should not have that severance in Amazonia of South America into two parts as claimed by some geologists. Whatever may have been the bearing,

<sup>1</sup>1912, Ann. N. Y. Acad. Sci., XXI, p. 32.



if any, of the entrance of the sea into Amazonia on the distribution of *Baryphthengus*, it seems evident that the range of this bird was not developed under existing topographic conditions, and this belief, in connection with the facts that *Baryphthengus* has extended its range farther into South America than *Momotus* and that it is apparently a somewhat more primitive type than that genus, leads to the conclusion that, while *Baryphthengus* is of northern origin, it entered South America at a much earlier period than did *Momotus*.

It is interesting to observe, though I am quite unable to explain the phenomenon, that *Baryphthengus ruficapillus* does not trim its central rectrices into the spatulate form present in most species of this family and thereby agrees with the primitive genera *Aspatha* and *Hylomanes*. But this singular fact loses much of its apparent taxonomic significance when it is learned that east of the Andes *B. martii* has also lost, or at least, lacks the tail-trimming habit, while west of the Andes its tail, normally, is spatulate.

The same inexplicable state of affairs exists in the allied genus *Electron*, in which the forms found east of the Andes (*E. platyrhynchus pyrrholæmus* and *E. p. medianum*) normally have the central rectrices entire, while in those found west of the Andes (*E. p. platyrhynchus*, *E. p. suboles* and *E. p. minor*) these feathers, in the adult, have racquet-shaped tips. Furthermore, in *Momotus momota momota* and *M. m. microstephanus* this habit is subject to individual variation.

#### GEOGRAPHIC ORIGIN OF THE GENUS *Momotus*

The present center of dispersal in Middle America of the genus *Momotus* appears to be in the Mexico-Guatemala region. Here the two distinct types of the genus are found, and from this point the rufous-crowned species (*mexicanus*) ranges northward into western Mexico, while the black-and-blue-crowned species (*lessoni* and *cæruliceps*) range northward into eastern Mexico. Moreover, it is only in Mexico that *lessoni* is restricted to the Tropical Zone, and it is in this zone that we must look for the ancestors of those species which inhabit altitudinal zones above the Tropical Zone. The chestnut-crowned *Momotus castaneiceps*, according to Salvin and Godman,<sup>1</sup> is found only on the plains of Zacapa in Guatemala, in "comparatively open country, large cacti and mimosa trees being the characteristic plants." If, therefore, the rufous-crowned species prefers haunts of this type, rather than

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<sup>1</sup>'Biol. Cent. Amer.,' II, p. 461.



the denser growth which *lessoni* frequents, it is clear why the former has found a favorable environment in more arid western Mexico, while *lessoni* has been equally at home in humid eastern Mexico.

For the same reason, possibly, *lessoni* has extended its range southward into Central America while the rufous-crowned species is unknown south of Guatemala. We are, therefore, not further concerned with the *castaneiceps-mexicanus* group and may concentrate our efforts on an attempt to trace the history of the black-and-blue-crowned species.

We have seen that as we proceed southward from the assumed place of origin of *lessoni*, in the Tropical Zone of southeastern Mexico, we find this bird extending its range to higher altitudes until in Costa Rica and Chiriqui it becomes a form of the Subtropical rather than of the Tropical Zone. Lack of field experience in Central America denies me that knowledge of topography and environment which comes only from direct observation, and I therefore am not prepared to discuss the causes which have induced *Momotus lessoni* to increase the altitude of its range as it approaches equatorial regions.

It occurs to me, however, that possibly we may have here governing conditions which, in some respects, resemble those that induce birds of the South Temperate Zone to mount to the Andean tableland as they extend their range toward the Equator.

If it could be shown that *lessoni* originated in the northern or subtropical portion of the Tropical Zone of eastern Mexico, we should then have some explanation of why it attempted to remain in this zone by increasing the altitude of its range as it proceeded southward.

Beyond Chiriqui, in western Panama, *lessoni* is unknown, but it is represented in the Subtropical Zone of all three ranges of the Colombian Andes, and southward to Peru by *Momotus æquatorialis*, a distinct species but apparently an unquestionable derivative of *lessoni*.

#### THE PANAMA SUBTROPICAL BRIDGE

At once we ask: How could a non-migratory, sedentary, cover-haunting bird like the motmot cross the 400-mile gap separating the Subtropical Zone of western Panama from the Subtropical Zone of north-western Colombia?

Fortunately, our studies of the distribution of bird-life in Colombia<sup>1</sup> furnish an answer to this query. These studies have shown that the ranges of between sixty and seventy species common to the Subtropical Zones of Colombia and Chiriqui-Costa Rica are broken by what I have

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<sup>1</sup>1917, Bull. Amer. Mus. Nat. Hist., XXXVI, pp. 151-159.



termed this Panama "fault." A number of them have also been found in the restricted subtropical areas of eastern Panama, but between that point and western Panama they are unknown. The list includes such sedentary species as *Formicarius rufipectus*, *Grallaricula flavirostris* and *Siptornis erythropus*, and species of such specialized habits as the dipper (*Cinclus*) or of such abundance and adaptability as the Andean white-throated sparrow (*Brachyspiza capensis*). In view of the data presented at length in the paper mentioned above, it seems unnecessary to go into further detail here and it may simply be added that the presence in the Subtropical Zones of Chiriqui and Colombia of so large a number of species, many of which are sedentary forms having a limited power of flight, is strong if not conclusive evidence that these regions were at one time connected by a Subtropical Zone bridge which, doubtless through subsidence, has disappeared in comparatively recent geological times.

Once in the Andean region, where it is the only member of its family found above the Tropical Zone, the subsequent extension of range of *Momotus æquatorialis* is an impressive exhibition of the influence of those potent factors which hold a bird to its proper faunal area. Always within the comparatively narrow limits of the Subtropical Zone, or approximately between the elevations of 4500–9500 feet, it has wound its way along the slopes of the Colombian Andes southward and northward until it now is found in all three ranges. It is not recorded from the Santa Marta group nor from Venezuela, and in spite of its presence in the Andes west of Popayan, it is as yet not definitely recorded from western Ecuador.

On the Amazonian slope of the Andes, *æquatorialis* has flowed south, as it were, in that narrow stream of life which so clearly distinguishes the subtropical element from the tropical below it and the temperate above it, at least as far as southeastern Peru near the Bolivian boundary. It has not yet been recorded from Bolivia, and if it does not occur there it has not yet reached the southern limit of the Subtropical Zone in the more eastern part of the Amazonian slope of the Bolivian Andes.

In Peru, *æquatorialis* exhibits some racial variation and is known as *Momotus æquatorialis chlorolæmus*, a form with greener underparts. But the difference between Colombian and Peruvian specimens is slight and bridged by individual variation.

In short, *Momotus æquatorialis*, like numerous other species of the Subtropical Zone, shows, in spite of its wide range, surprisingly little variation and thereby gives expression to the uniform environmental conditions which prevail throughout this remarkable faunal stratum.



To sum up: The evidence in regard to *Momotus æquatorialis* indicates (1) that it was derived from *Momotus lessoni* and thus originated in eastern Mexico; (2) that it entered South America subsequent to the full development of the Andean System; (3) that the subtropical "bridge" on which it crossed Panama has since disappeared; (4) that its subsequent distribution eloquently illustrates the potency of the influences which determine the boundaries of life-zones and (5) that there have been no marked changes of level in the Andes since it reached them.

#### THE SPECIES OF THE TROPICAL ZONE IN SOUTH AMERICA

Having presented and considered the evidence in regard to the origin and distribution of the *lessoni-æquatorialis* group, we may now turn our attention to the remaining species of the group, all of which, except *subrufescens* which is found in Panama, are confined to the Tropical Zone in South America.

*Momotus subrufescens* has been found as far west in Panama as the Canal Zone, but there is no reason why it should not be found throughout the Tropical Zone of that country. While not distantly related to, it is apparently specifically distinct from *lessoni* of the Subtropical Zone of western Panama, and with it we enter a new section of the genus *Momotus* and are at once confronted by the problem of its origin.

Since *lessoni* finds its South American representative in *æquatorialis*, we cannot look direct to that species for the ancestral form of *subrufescens*, but possibly we can look indirectly to it and discover the origin of *rufescens* in the pre-*lessoni-æquatorialis* form which once occupied the Panama bridge connecting the Subtropical Zones of Chiriqui and Colombia.

It is true that the survival of this form would be contrary to the rule which has evidently prevailed among the birds with which we assume this connectant, subtropical form was associated. But it is also true that the motmots are with but two exceptions confined to the tropics and that *lessoni* shows its adaptability by inhabiting both the Tropical and Subtropical Zones in Central America. It is not, therefore, beyond the bounds of reason to assume that the connecting, "bridge"-inhabiting form might adapt itself to changing environmental conditions as subsidence gradually lowered its range from the Subtropical to the Tropical Zone.

It is true that *æquatorialis* has extended its range from Colombia to southern Peru without showing as much racial difference as *subrufescens* does from *lessoni*, and hence presumably from its supposedly extinct ancestor. But, as I have attempted to show<sup>1</sup> in comparing the birds

<sup>1</sup>'The Distribution of Bird-Life in the Urubamba Valley of Peru,' 1921, U. S. Nat. Mus., Bull. No. 117, pp. 30-35.



of the humid Temperate Zone with those of the Puna Zone in southern Peru, it is the extent of environmental change, not time or distance, which supplies the more potent evolutionary factors.

It is therefore to be expected that a change from the Subtropical to the Tropical Zone would be followed by more marked changes in the organism than continued residence in the Subtropical Zone even at widely separated stations.

This theory of the origin of *subrufescens* confessedly rests on a slight foundation of fact, but it is the only one that presents itself, and, since the distribution of this species is apparently from the north southward, we cannot well look for its ancestor in South America.

From Panama the range of *subrufescens* extends eastward into Colombia and the coast region of Venezuela to Trinidad, but it does not extend southward to western Ecuador, where a quite different species of *Momotus* is found.

Specimens from the semi-arid Caribbean coastal region (*rufescens rufescens*), as we have seen, are paler, less intensely colored than those from the more humid, forested areas of Panama, the Atrato and Magdalena Valleys, southern Maracaibo basin, Trinidad and Tobago, but it is evident that we have here but one responsive form, the differentiating characters of which have been derived under existing environmental conditions. When, however, we compare the extreme humidity of eastern Panama and the Atrato Valley with the comparative aridity of the Venezuelan costal region, it is apparent that climatic conditions under which *Momotus subrufescens* lives vary more widely than does the bird itself. Hence we conclude that either the environing conditions have not been in existence for a sufficient length of time fully to express themselves on the bird, or that the bird has not been exposed to them long enough fully to respond to their influences. However, the restriction of the area occupied by *subrufescens* to western Colombia and the Caribbean coast region induces the belief that it is of post-Andean origin (a conclusion supporting our theory of its descent from the pre-*lessoniæquatorialis* type) and that consequently its range has been acquired under present topographic<sup>1</sup> and hence doubtless climatic conditions.

The response of the various forms of *subrufescens* to the climatic influences which we believe to have produced their distinguishing characteristics not only furnishes an admirable illustration of cause and effect and an indication that the species is in an active state of evolution,

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<sup>1</sup>Trinidad, however, was probably connected with northeastern Venezuela and Tobago with Trinidad when the bird entered the territory which has since become insulated.



but gives additional proof of its comparatively late entrance into the region it inhabits.

In western Colombia *subrufescens* is unknown south of the Atrato Valley. Possibly it may occur farther south but it certainly does not reach western Ecuador, where its place is taken by *M. momota argenticinctus*, a close ally of *M. m. microstephanus* of the eastern base of the Colombian (and Ecuadorian?) Andes. This is, however, not the only case where the form of the Tropical Zone of western Ecuador is related to that of the east Ecuador Tropical Zone rather than to that of Panama.<sup>1</sup>

We now cross the Andes and take up the *Momotus momota* group.

#### The *Momotus momota* Group

The Tropical Zone of the Panama-Caribbean region is connected with the Tropical Zone of that part of South America lying east of the Andes only in northern Venezuela. Whether *subrufescens* enters the interior of Venezuela is unknown.

The bird of the lower Orinoco is *Momotus momota momota*, a form which, whatever its origin or relationships, certainly does not intergrade directly with *subrufescens*. If, therefore, the ancestors of the *momota* group entered the interior of South America through the north Venezuelan Tropical Zone connection, their further progress was presumably not toward the Orinoco, but westward along the base of the Andes toward the region now occupied by *microstephanus*. This question cannot be discussed profitably until we know what form of motmot inhabits the region between the Orinoco and the known range of *subrufescens* in northern Venezuela. Meanwhile we may consider the possibility of an Andean crossing in the comparatively low area at the head of the Magdalena Valley. Our records show the occurrence of *Momotus subrufescens conexus* at Chicoral in the upper part of this valley. If the species could exist in the limited, scrubby growth of this region, there is no reason to doubt its occurrence up to the head of the Valley.

Our explorations in Colombia have shown that the eastern Andes at Andalucia attain an altitude of only 7000 feet. They also show that this elevation has not been great enough to prevent the entrance into the upper Magdalena Valley of several forms from the Tropical Zone at the eastern base of the range. Examples are, *Piaya cayana mesura*, *Conopophaga castaneiceps castaneiceps*, *Myiobittacus phœnicurus*, *Tangara chilensis*, and *Tangara cyaneicollis cæruleocephala*, all of which are known from west of the Andes only in the upper Magdalena Valley. The fact

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<sup>1</sup>See 'Distribution of Bird-Life in Colombia,' pp. 106-117.



that neither *Baryphthengus* nor *Electron* is found in northern Venezuela indicates that they have reached the interior of South America by crossing the eastern Andes of Colombia (see the map illustrating the distribution of *Baryphthengus*).

While the frequent occurrence of parallelism in *Momotus* and particularly in *M. subrufescens* (note the recurrence of dark forms in separated humid areas) warns us not to place too great significance on superficial resemblances as indicating sources of derivation, it is nevertheless true that in general coloration the form of *subrufescens* found in the Magdalena Valley shows an approach toward the form inhabiting the Tropical Zone at the eastern base of the Andes. Indeed, the differences between them are obviously not greater than those which distinguish many intergrading forms.

The evidence at our disposal, therefore, makes it within the bounds of probability that the *Momotus* group entered the interior of South America over the Subtropical Zone pass in the eastern Andes of Colombia. The assumption that eastern Colombia has been its point of dispersal finds support in its distribution. In the systematic portion of this paper we have seen that *microstephanus*, the east Colombian form, possesses certain characters which indicate its close relationship with *momota*, with which it is believed to intergrade. In the east, therefore, in the area bounded on the south by the Amazon and on the north by the Valley of the Orinoco, we have but one form which, in its combination of characters of size, markings, and non-spatulate central rectrices, is the most strongly differentiated of the entire group. The lower Amazon has been shown to be an effective barrier to the extension of the range of this species, preventing its contact with the quite different *simplex* at Santarem on the southern side of the river; and I have ventured to express the belief that the races described from the Pará region represent not *momota* but *simplex*.

To the south, *microstephanus*, believed to be the ancestral form of the *momota* group, responds to the widely varying conditions it encounters in the enormous area it now inhabits, and to these expressions of the influences of its environment have been attached the names *ignobilis* in Peru, *nattereri* in Bolivia, *pilcomajensis* in northern Argentina and contiguous Bolivia, *simplex* in central Brazil and *parensis* and *cametensis* in the Pará region. The more important facts revealed by our study of its variations and distribution south of the Amazon are (1) the divergence of the forms of the right bank of the lower Amazon from that of the left bank, which, although they have apparently descended from a common



ancestor, would possibly meet as species. (2) The continuous distribution of the species through the area it inhabits and the evident intergradation of all its forms, as indicating their origin under existing environmental conditions. (3) That, notwithstanding the presumably longer period which *Momotus æquatorialis* of the Subtropical Zone has been in South America, it exhibits far less variation in its range from Colombia to southern Peru than does *momota* in the contiguous Tropical Zone, a fact which is believed to reflect the much higher degree of uniformity prevailing in the Subtropical as compared with the Tropical Zone. (4) That, in spite of the absence of any physical or climatic barrier to range extension, the species has not yet reached the forests of southeastern Brazil and Paraguay, a fact which is believed further to indicate its comparatively recent appearance in South America.

We have seen that the western Ecuador form occupies the Tropical Zone from at least Esmeraldas south to northwestern Peru and that it finds its nearest ally, with which it intergrades by individual variation, not in western Colombia, as might be expected, but in the Tropical Zone at the eastern base of the Andes. We have also seen that the known facts concerning the distribution of *Momotus* indicate that it is of post-Andean origin in South America. From these premises we are forced to conclude that, just as the ancestor of *microstephanus* crossed the Andes from west to east, so the ancestor of *argenticinctus* crossed the Andes from east to west. But we cannot believe in this case, any more than we could believe in that of *microstephanus*, that this presumed transandean passage was made where the mountains attain a sufficient altitude to permit of the development of a Temperate Zone. In Ecuador, therefore, as in Colombia, we look for some lower elevation over which it is conceivable the species might extend its range.

The nearest approach to such a condition is apparently to be found in the cañon of the Rio Zamora, which enters the Loja Valley from the Tropical Zone of Amazonia at an altitude of not more than 7000 feet. From the Loja Valley the Pacific slope may have been reached by following one of the streams having their origin in this valley and flowing into the Pacific. It is true that existing conditions of vegetation in the Loja Valley do not support this theory, but it is also true that in the historic period this valley has been deforested for agricultural purposes and that consequently there was formerly much closer connection between the forested areas of eastern and western Ecuador than is to be found at present.



While this paper is going through the press our collector, Harry Watkins, writes us of his capture of motmots (doubtless *M. m. argenticinctus*) at Palambla on the western slope of the Andes, between Payta and Huancabamba, Peru. This is the most southern point on the Pacific Coast from which motmots have been recorded and also the nearest one to Amazonian drainage. The work of Noble<sup>1</sup> about Huancabamba shows a marked affinity between the avifaunas of that region and southwestern Ecuador, and it is hoped that Watkins' researches will throw much additional light on the possibility of a faunal connection between the Pacific coast and Amazonia in this region.

#### SUMMARY

The theories advanced and the principal conclusions reached in this paper may be summarized as follows.

1.—The motmots originated in Central America, where the ancestral forms of the existing genera were possibly developed during the Oligocene when this region consisted of scattered islands which would afford the isolation favorable to differentiation.

2.—The characters and distribution of the genera *Hylomanes* and *Aspatha*, and the relationships of the former with the West Indian family Todidæ, indicate that these genera are the most primitive known members of the family.

3.—The characters and distribution of the genus *Momotus*, which is represented, usually by intergrading forms, throughout the greater part of the area occupied by the family, indicate that it is the most recently evolved member of the family.

4.—Long after the more primitive forms of the group (*Hylomanes* and *Aspatha*) were evolved, on three occasions the family has invaded South America.

5.—The first of these invasions, made by the genus *Baryphthengus*, was possibly pre-Andean or early Tertiary, and extended to southeastern Brazil where the representative of the group was subsequently isolated by causes as yet unknown.

6.—The second invasion was made by the genus *Momotus*, and was subsequent to the elevation of the Andes and not earlier therefore than the later Tertiary, from the Subtropical Zone of the mountains of Costa Rica to the same zone in the Andes of northwestern Colombia over a Panama connection between these zones which, through subsidence, has since disappeared. From northwestern Colombia the species has

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<sup>1</sup>Bangs and Noble, 1918, Auk, XXXV, pp. 442-463.



spread southward through the Andean Subtropical Zone to southeastern Peru.

7.—The third invasion was also made by the genus *Momotus* and was subsequent to the period of subsidence which brought the mountains of Panama below the elevation of the lower limits of the Subtropical Zone. It extended from Panama through northern Colombia and Venezuela, north of the Andes, to Trinidad and Tobago when these islands were connected with each other and with the mainland.

The Andes were crossed probably at the head of the Magdalena River and the genus now occupies the greater part of tropical South America, its recent entrance into this region being indicated by the continuity of its distribution, the comparatively slight degree of differentiation it exhibits, and the fact that, although the environment is favorable, it has not yet reached southeastern Brazil.

If, in the main, these conclusions are valid, they will be of much service in our attempt to determine the geographical origin of South American bird-life, and particularly of the highly developed faunas which characterize Andean life-zones.







**Article III.**—SOME SKULLS OF *PERCHÆRUS* [*THINOHYUS*]  
FROM THE WHITE RIVER AND JOHN DAY FORMATIONS

BY HELGA S. PEARSON

In The American Museum of Natural History there are five primitive suilline skulls from the White River and John Day Oligocene; in all of them the lower jaw is lacking, but otherwise they are nearly complete. Besides these there are the back part of another skull and a variety of jaw fragments.

Two of these skulls have already been described by Cope (1888, Proc. Amer. Phil. Soc., XXV, pp. 70–77) under the names *Bothrolabis pristinus* and *B. rostratus*. Sinclair determined (1905, Univ. of Californ. Publications, Bull. Dept. Geol., (6) IV, p. 135) that Cope's genera *Chænohyus* and *Bothrolabis* were identical and synonymous with Marsh's type *Thinohyus* (Marsh, 1875, Amer. Journ. Sci., (3) IX, pp. 248–249). Peterson expressed a similar opinion (1905, Mem. Carneg. Mus. Pittsburgh, (8) II).

In 1907 (Bull. Amer. Mus. Nat. Hist., XXIII, p. 216) Matthew established a new genus, *Desmathyus*, for certain Lower Miocene suillines intermediate in type between the specialized dicotylids of higher levels and the primitive Oligocene genus *Perchærus* Leidy (Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2) VII, p. 195). He pointed out that Peterson's species "*Thinohyus*" *siouxensis* (Peterson, *loc. cit.*), from the Harrison beds of the Lower Miocene, could more properly be referred to this new genus, whereas the typical *Thinohyus*, from the John Day Oligocene, was apparently not generically distinct from the White River *Perchærus*.

In 1915 Cope's plates of the species described by him for the U. S. Geological Survey were published with descriptions by Matthew, who revised the generic names "*Palæochærus*," "*Bothrolabis*," and "*Thinohyus*" to *Perchærus* ('Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrates,' U. S. Geological Survey and Amer. Mus. Nat. Hist., Monograph Series, No. 2).

Dr. Matthew felt that the Oligocene material in the American Museum needed more detailed description and he very kindly suggested that I might undertake the work. I should like to offer my very best thanks to the following for the help which they have given me in the course of this paper. To Dr. W. K. Gregory for his advice and criticism, for reading the manuscript, and for the privileges which I have enjoyed in his department. To Dr. W. D. Matthew for reading the manu-



script and for the free access which I have had to the material under his charge. To Mrs. Helen Ziska for her valuable suggestions and criticism in drawing. And to Miss Jannette M. Lucas and my other friends of the American Museum library for incalculable assistance, moral and material.

#### THE SKULL OF THE GENUS *PERCHÆRUS*

Stehlin, in his monograph 'Ueber die Geschichte des Suiden Gebisses' (Zurich, 1899), attempted to compare Cope's John Day "Bothrolabidæ" with recent peccaries and to gain some light on the relationships of New World to Old World suillines. He had only Cope's figures and descriptions of the John Day skulls to be guided by and, as he himself pointed out, these were inadequate as regards morphological detail.

Descriptions of the New World Oligocene suillines by American writers would seem to have been so exclusively concerned with allotting them to one or other of the numerous species which have arisen, or with creating new species, that the well-established underlying structure which they have in common has been neglected. In our ignorance as to the degree to which even closely related individuals can vary from one another, a study of such superficial characters as are usually relied upon for separating species is, especially in dealing with fossil material, of very little value in tracing relationships.

It may, therefore, be of some help towards an understanding of the relationship between New World and Old World suillines to give here a description of certain characteristics which seem to have firmly established themselves in a number of the earliest known skulls of the former.

An idea of the general shape and proportions of the skulls and their component parts may best be obtained from the figures. I will, therefore, give a detailed description of only the more interesting regions.

#### BASICRANIAL AND OTIC REGIONS

In the otic region *Perchærus* is already well advanced along the line of specialization peculiar to the suilline group (though paralleled in other widely divergent groups such as the rhinoceroses and certain rodents); that is to say, the post-glenoid and post-tympanic processes of the squamosal have closed around the tubular external auditory meatus, forming a sheath which fuses with the tympanic. In later forms this sheath extends half-way up the side of the occiput, carrying with it the opening of the middle ear, but in *Perchærus* it still does not extend much above the level of the top of the foramen magnum. A clear understand-



ing of this region can best be obtained by tracing its structural evolution from a primitive Eocene artiodactyl through Oligocene forms of other groups which have not in this part of the skull advanced so far on their own peculiar line of specialization as has *Perchærus*.

Fig. 1 is a ventral view of the incomplete and crushed skull of a Bridger bunodont artiodactyl, A. M. N. H. No. 13079, probably referable to the genus *Helohyus* (Sinclair, 1914, Bull. Amer. Mus. Nat. Hist., XXXIII, p. 283). Here the tympanic bone is lacking and was

probably, as in the Eocene members of other mammalian groups, ring-shaped, or at any rate not completely flask-shaped, and not firmly ankylosed with the neighboring bones of the skull. The stout paroccipital process is composed of a broad exoccipital portion posteriorly, and anteriorly of a well-developed mastoid, the grooved ventro-mesial surface of which doubtless served as a channel for the facial nerve,



Natural size.

Fig. 1. Basis cranii of ? *Helohyus*, No. 13079.

though I have been unable to detect the opening of the aqueductus fallopian in the periotic bone. On the exposed surface of the latter a large fenestra rotunda is evident and just in front of this there is a smaller fenestra ovalis, lying directly opposite the mouth of the deep, empty channel between the post-glenoid and post-tympanic processes of the squamosal. The post-glenoid process, a downwardly-projecting flange at the back of the flat glenoid surface of the squamosal, is penetrated by a large post-glenoid foramen. (This foramen, if it corresponds to the similarly situated one which in most recent mammalian groups closes up during embryonic life, indicates the primitive condition of an external jugular vein communicating anteriorly with the venous sinuses within the cranium.) The post-tympanic process, forming the posterior wall of the channel, is another downwardly-directed flange and is pressed against the anterior surface of the root of the mastoid.

Fig. 2, of the otic region of *Leptomeryx evansi*, A. M. N. H. No. 1343, represents a type which is primitive and generalized for White River artiodactyls, since they all, except the extremely aberrant entelodonts, can be readily referred to it. The chief advance over the Bridger forms



is in the flask-shaped tympanic, firmly ankylosed to the surrounding bones, with its tubular neck lying wedged into the channel between the post-glenoid and post-tympanic processes of the squamosal; its rounded bulla fails to cover completely the ventral surface of the periotic, the mesial edge of which lies exposed between it and the basi-occipital. The mastoid still forms a considerable portion of the paroccipital process and the groove on its mesial surface is now closed in by the tympanic bulla to form the stylomastoid foramen. The postero-ventral surface of the bulla, just in front of and mesial to this foramen, has a deep pit-like indentation plugged by the small wedge-shaped tympano-hyal. There is apparently no post-glenoid foramen.

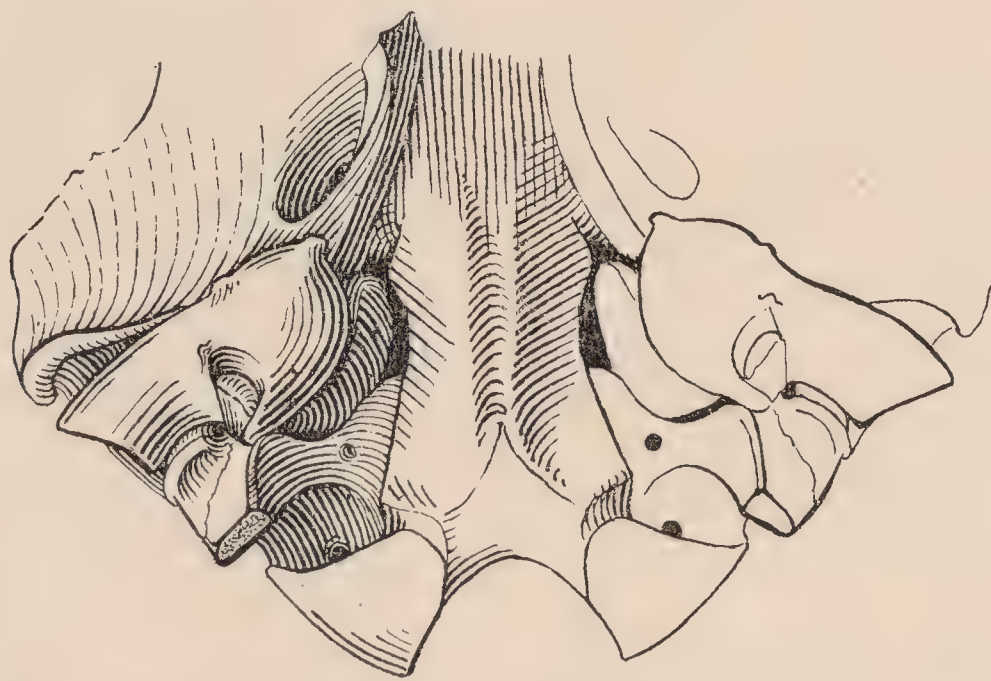


Fig. 2. Basis cranii of *Leptomeryx evansi*, No. 1343.

One and a half natural size.

Returning to the skulls of *Perchaerus*, we find the otic region most completely shown in Nos. 7394 and 7398 (Figs. 3 and 12), though it is sufficiently well preserved in the other skulls and especially in the two young ones from the White River (Fig. 6) to complete the information given by these and to show that all are essentially similar in this region. The tubular external auditory meatus no longer lies freely exposed on the ventral surface of the skull, but the channel in which it rests, between the postglenoid and post-tympanic processes of the squamosal, has become closed in to form a complete tunnel by the fusion of these two processes along its whole length. The floor of the tunnel is formed by the post-tympanic process, which curves forward beneath the bony meatus and laps up against the posterior surface of the post-glenoid process. The two processes have fused with each other and with the enfolded bony meatus itself. Although there is apparently no post-glenoid foramen leading into the brain cavity, the post-glenoid process is pierced by a narrow



tunnel running through it from side to side. This tunnel, which is present in more recent peccaries but not in *Sus*, lies nearly parallel to the auditory meatus, which runs upwards, outwards and backwards from the cavity of the bulla. The lateral opening of this tunnel is by the side of, and just anterior to, the auditory opening itself and lies with the latter at the base of the same shovel-shaped pit at the back of the zygomatic process of the squamosal (Fig. 4). The mesial opening is just above the level of the ventral surface of the bulla and lies two-thirds of the way back along the length of the latter, which is here joined to the post-glenoid process by a narrow bridge or bone. In front of this bridge there is a pit-like depression, exceptionally deep in No. 7398, between the

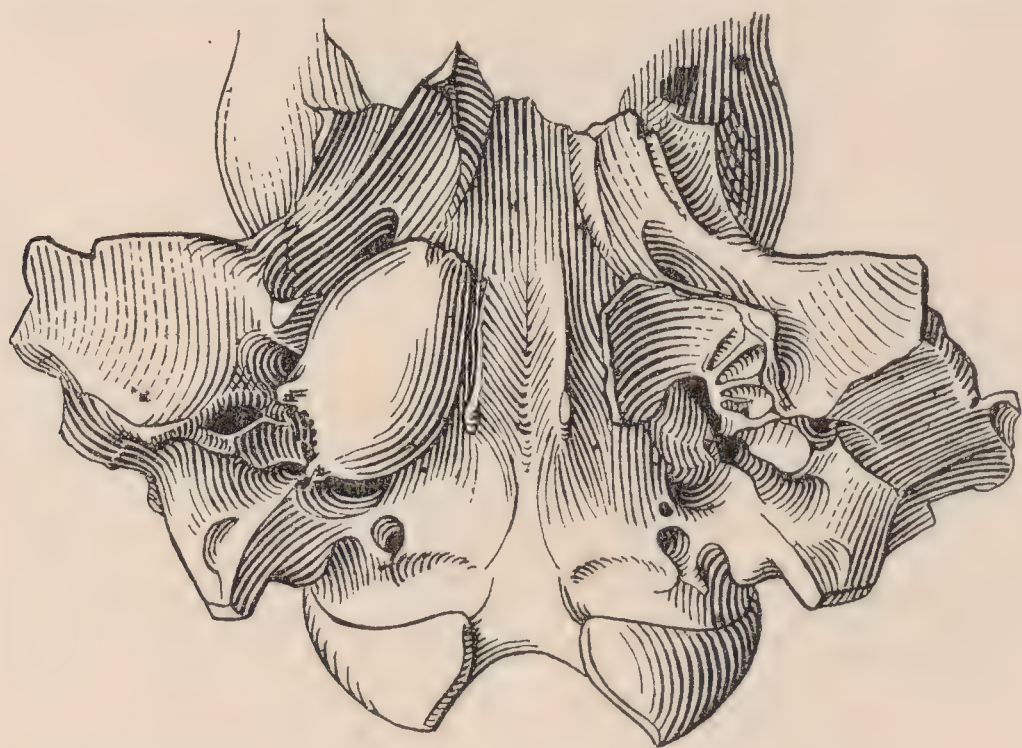


Fig. 3. *Perchærus* species, No. 7398.

Three-quarters natural size.

side of the bulla and postero-mesial corner of the glenoid surface. A much deeper pit lies directly behind this bridge and, although no tympano-hyal is present, its relation to the surrounding structures indicates that this is where the tympano-hyal was lodged and that the bridge itself and the prominence which projects back from it on the outer side of the pit correspond to that part of the bulla which in *Leptomeryx* (Fig. 2) ensheaths the tympano-hyal plug antero-laterally. Immediately behind this region, again, is the stylomastoid foramen, forming the mouth of a channel which leads upwards into the tympanic cavity.

The mastoid process, as in recent suillines, has disappeared<sup>1</sup> and this channel for the facial nerve, instead of forming a groove on the mesial

<sup>1</sup>Gidley, J. W. (1920, Proc. U. S. Nat. Mus., XLVII, p. 654) appears to mistake the post-tympanic process of the squamosal for a true mastoid. Disarticulated young skulls of *Tayassu* and *Sus* show that the periotic has no pars mastoidea. In this paper Gidley gives definitions of the families Suidæ and Tayassuidæ and of the two recent tayassuid genera *Tayassu* and *Pecari*.



surface of that process in the primitive manner, makes a groove instead on that part of the squamosal which takes its place. That is, the part lying behind the post-tympanic process and abutting against the anterior face of the paroccipital process of the exoccipital (Figs. 6 and 7).

The bulla itself is roughly egg-shaped, its long axis antero-posterior and at only a very slight angle with the plane of the basis cranii, its narrower end rugose and pointing forwards. It completely covers in the periotic bone ventrally, there being but a narrow crack between its mesial wall and the basi-occipital. At its posterior end, however, the edge of the latter bone is scooped out in the usual way to form the foramen lacerum posterius or jugulare; this foramen, in contrast to the condition found in *Tayassu* but in accordance with that in most primitive forms, is completely separated from the stylo-mastoid foramen by a backward projection from the tympanic bulla meeting a forward projection from the root of the paroccipital process.

Although the bulla was apparently not filled with a dense sponge of cancellous bony tissue, as in *Desmathyus* and more recent peccaries, there are traces of bony septa on its inner surface in some of the skulls (Figs. 3 and 6).

The paroccipital process (see especially Figs. 6, 11, and 13) is of the dicotyloid type, of moderate length only and with pointed extremity and broad base. It is more flattened antero-posteriorly than in *Tayassu*, however, with strongly ridged edges. The postero-internal edge takes origin in the narrow prominence separating the jugular foramen (f. lacerum posterium) from the condylar foramen. Just below its origin this edge is produced into a small backwardly-directed process.

There is a single condylar foramen only, large and corresponding in position to the anterior one of other forms.

The configuration of the muscle areas on the basi-occipital surface and the prominence of their bounding ridges varies somewhat in the different skulls. I have found this region to be very variable in *Tayassu*, also among skulls of the same sub-species. All the *Perchærus* skulls show, however, two more or less well-marked ridges at the anterior end of the bone, between the tympanic bullæ, for the insertion of the longi capitis muscles; these ridges are best developed in No. 7398 (Fig. 3).

#### OCCIPUT

Fig. 4 is a reconstruction of this region made from the two White River skulls and from the young skull (No. 7396) from the John Day, which corresponds very closely with them.



The supra-occipital region, which in recent suillines is flattened outwards by the extensive parietal sinus within, is here much more deeply hollowed beneath the occipital crest; a median ridge runs up it for some way from the dorsal border of the foramen magnum below. This dorsal border is notched in the mid-line where the supra-occipital is just excluded from it by the two exoccipitals meeting each other.

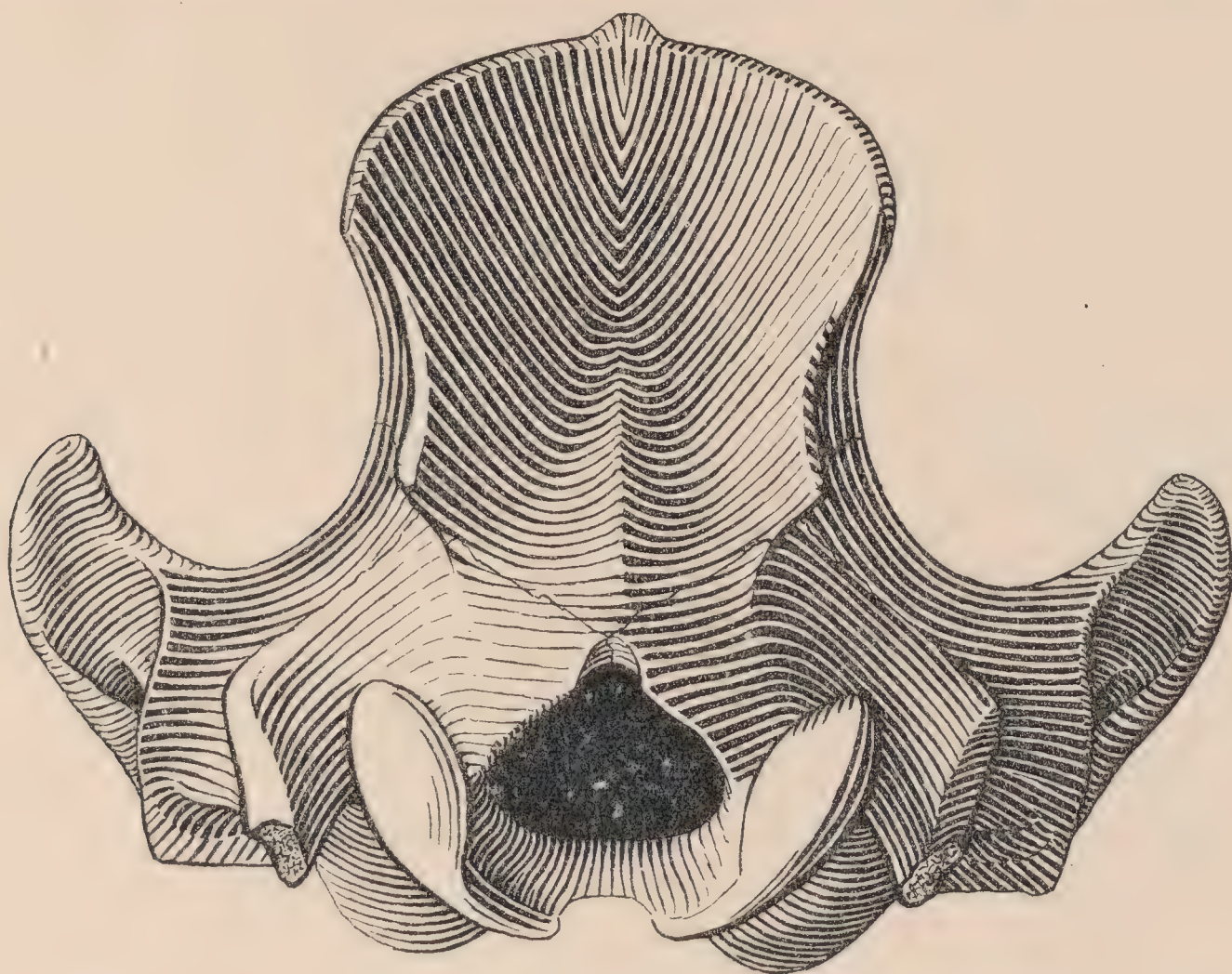


Fig. 4. Occiput of *Perchærus* as reconstructed from the young White River skulls, Nos. 585 and 695.

Natural size.

The hollowed-out appearance of the back of the occiput is accentuated by the presence on either side of it of a crest which joins the main occipital crest above and runs straight down from the latter, to end abruptly in an outward projection about a centimeter above the exoccipital condyle.

The temporal fossa is divided from the occipital surface by the usual sharp ridge. This runs downwards and outwards from the occipital crest to form the postero-dorsal border of the zygomatic wing of the squamosal, and terminates in the cowl-shaped projection of the latter above the external auditory meatus.

#### GLENOID SURFACE AND ZYGOMA

The level of the glenoid surface of the squamosal, in comparison with the basis cranii and the ventral surfaces of the bullæ, appears to



vary with age and with species, but it is never so far depressed as in more recent peccaries (*Desmathyus* seems to have reached an extreme of depression). The surface is directed more from side to side than in these latter and there is not such a well-marked pre-glenoid elevation of the squamosal. Postero-externally this surface is smoothly continuous with a shallow depression which leads round from it up on to the lateral surface of the zygoma, parallel to the suture line between the post-glenoid and post-tympanic processes; there is no such depression in recent peccaries, where the glenoid surface is marked off posteriorly by a definite edge, joining the post-glenoid and pre-glenoid processes.

The zygomatic bar of the jugal has a strongly ridged ventral edge terminating abruptly just in front of the glenoid surface; this is more like the condition in *Sus* than that in later peccaries. Dorsally the jugal has the usual well-marked post-orbital process projecting up towards the post-orbital process of the frontal.

#### PALATE

From in front of each tympanic bulla the pterygoid process of the alisphenoid runs forwards to meet the sphenoid process of the palatine and together they form a long wall joining the palate to the basis cranii. This wall, with its fellow of the opposite side, encloses a long deep "mesopterygoid" fossa into which the posterior nares open anteriorly and the basisphenoid steeply plunges down posteriorly. In the John Day skulls the everted ventral edge of this wall carries a double ridge with a shallow groove between; this is the pterygoid fossa for the internal pterygoid muscle; it leads up to the mouths of the foramen ovale and the foramen lacerum medium under cover of the anterior end of the tympanic bulla. (The foramen ovale is completely encircled by alisphenoid in all the skulls of *Perchærus* which show this region clearly, and is not, as in recent suillines, merely a notch confluent behind with the foramen lacerum medium.)

In *Desmathyus* the two well-separated walls of *Perchærus* have been, as it were, pinched together, the posterior nares being thus thrown much farther back. A similar condition is found in the modern genus *Pecari*, whereas in *Tayassu* and most of the Pleistocene forms the position of the nares can better be described as due to the backward extension of the palate.

There is no evidence of the presence of a pterygoid bone.



## ORBIT

*Perchærus pristinus*, No. 7394, is the only skull which shows this region well, so that the description given is mainly from this (see Fig. 5). Such structure as is preserved in the other skulls, however, fits in essentially with this; *P. rostratus*, No. 7395, diverges most in detail from the type, as in all other parts of the skull.

The most conspicuous feature of the orbit of *Perchærus* is, perhaps, its prominent lachrymal bulla. This protrudes into the antero-external corner of the orbit at the root of the zygomatic arch. It is formed by the orbital part of the lachrymal bone and joins the jugal by suture laterally, the maxilla ventrally. A sharply defined ridge curves down its orbital surface from the lachrymal foramen above to the posterior opening of the infra-orbital canal below.

The lachrymal foramen is situated within the anterior edge of the orbit, just above the bulla; it lies in a pit under cover of a small lachrymal tuberosity. Mesial to it, on the mesial border of the lachrymal bone and well within the orbit, lies another pit or depression; this is too much crushed and distorted in all the skulls to lend itself to clear description, but it probably corresponds to the similarly situated pit which in recent suillines gives origin to the interior oblique eye muscle. See Sisson, 'The Anatomy of the Domestic Animals,' 2nd edition, p. 172.



Fig. 5. Orbit of *Perchærus pristinus*, No. 7394, as seen from without and behind.

One-half natural size.

Gregory (Bull. Amer. Mus. Nat. Hist., XLII, p. 193) refers to this pit in the recent peccary as a prominent foramen possibly representing the spheno-palatine foramen and leading into the nasal cavity. The true spheno-palatine foramen in *Tayassu*, however, is that which lies between the vertical plate of the palatine and the orbital expansion of the ethmoid, just below and in front of the latter at the entrance of the infra-orbital canal. The foramen in question would seem to be rather a perforation or break in the very thin bone lining the pit, and is not present in all the skulls in the Museum collection; it is probably always closed up in the living skulls. Since the pit corresponds almost exactly in position with that described by Sisson as housing the inferior oblique muscle in *Sus*, it is presumably homologous with that in both *Tayassu* and *Perchærus*.



The similarity between *Perchærus* and *Sus* in this region is striking, in spite of the absence of a definite lachrymal bulla in the latter. They not only agree in the possession of lachrymal foramina and of the above-discussed pit in the lachrymal, but in *Sus* as in *Perchærus* there is a strong ridge lateral to the pit and curving downwards from the vicinity of the lachrymal foramen to the orbital opening of the infra-orbital canal.

This region differs from that in ruminants, which also possess a lachrymal bulla, owing to the absence of the prominent circum-orbital rim of bone which in these prevents the bulla from appearing in a side view of the skull. The relations of the lachrymal bulla to the alveolar tuberosity of the maxilla also differ in *Perchærus* and the ruminants, because in the former, with its narrower palate, the tuberosity is very close to the sphenoid process of the palatine, whereas in the latter it is widely distant and immediately ventral to the bulla.

In *Perchærus* the alveolar tuberosity, the pointed posterior extremity of which projects back behind the third molar to the region of the palato-alisphenoidal suture, closes in the orbit ventrally, its dorsal surface forming a flat shelf. In the angle between this shelf and the lachrymal bulla is a deep crevice in which lies the entrance to the infra-orbital canal (maxillary foramen). The speno-palatine foramen appears to be a smaller opening which, as in *Tayassu*, lies just above and mesial to this entrance, but not, as in *Sus*, well forward within the canal itself.

The ethmoidal bone has not the bullate orbital expansion which in *Tayassu* lies postero-dorsally to the speno-palatine foramen and overhangs the fossa for the external pterygoid muscle. The orbital wall is concave in this region, but more posteriorly. Below the small ethmoidal foramen there is a slight swelling in the orbito-sphenoid, which probably marks the termination of the lateral ethmoid in the sphenoidal sinus.

A ridge runs from the tip of the maxillary tuberosity upwards and backwards towards the foramen speno-rotundum and delimits dorsally the area of origin of the external pterygoid muscle. Sutures are barely traceable in this region but the ethmoidal foramen is distinguishable on some of the skulls and presumably lies, as in recent suillines, in the orbital plate of the frontal, and marks the anterior end of the cerebral hemisphere at the level of the rhinal fissure.

At the back of the orbit there is an abrupt outward projection of the cranial wall, curving downwards from the post-orbital process of the frontal bone above to the root of the pterygoid wing of the alisphenoid below. This projection sharply separates the orbit from the temporal



region of the skull, and roughly marks the division between the anterior and mesial cranial fossæ within. It overhangs the foramen opticum and the f. spheno-rotundum (the latter formed, as in recent suillines, by confluence of the sphenoidal fissure and f. rotundum) situated at the back of the orbit. To the lateral border of the f. spheno-rotundum a ridge runs down the face of this projection, starting just below the entrance to the supra-orbital canal which lies directly under and in front of the post-orbital process. Less than a centimeter behind this ridge, and separated from it by a shallow groove, lies a second ridge, the infra-temporal or "pterygoid" crest, which starts immediately behind the post-orbital process in the region of the fronto-parietal suture; after crossing the suture between alisphenoid and squamosal, it ends perpendicularly to the anterior edge of the glenoid surface, about half a centimeter external to the edge of the pterygoid wing of the former bone. As it passes behind the foramen spheno-rotundum this second ridge is expanded, at the posterior edge of the temporal wing of the alisphenoid, into a pyramidal process (see especially Fig. 3 of No. 7398).

#### SNOUT

On the side of the face in front of the orbit there is absolutely no trace of the fossa in which, in recent suillines, lie the levator labii muscles controlling the mobile snout. The lachrymal bone has a well-developed facial plate which extends forward to a varying degree in the different skulls; it meets the maxilla anteriorly and divides the jugal from the frontal. From its sutures with the jugal and lachrymal the maxilla has a flat surface, smoothly continuous with that of those bones behind and of the frontal and nasal above, and sloping inwards towards the post-canine region. In front of this region, which is the narrowest part of the snout, the maxilla curves outwards again round the root of the canine. Just anterior to the latter it meets the premaxilla and the alveolar borders of the two are pressed upwards, in the adult skull, as though by the tip of a finger, to receive the tip of the lower canine.

The alveolar and palatal regions of the premaxillæ are bent downwards at a slight angle with the plane of the rest of the palate, as in more recent peccaries.

#### UPPER DENTITION

Except for a right upper permanent incisor, with only its tip exposed, in the young White River skull No. 695, the upper incisor teeth are missing in all the American Museum skulls. The only upper incisors preserved in any of the material are those in the type specimen of *P. trichæ-*



*nus* Cope, A. M. N. H. No. 7390 (Fig. 14), a much crushed and battered upper and lower jaw described separately below; it shows, as do the broken roots in *P. probus*, No. 1282, and the empty alveoli in other specimens, that the three incisors were of approximately equal size.

The canines are of the prominent, downwardly-directed dicotyloid type, flattened anteriorly and rounded or with a more or less sharp edge posteriorly. The outer surfaces bear one or more grooves.

P<sup>1</sup> and p<sup>2</sup> are narrow and two-rooted. [In "*Thinohyus*" *subæquans*, according to Cope and Peterson, p<sup>1</sup> is single-rooted.] Each consists of a protocone with a slight posterior heel. P<sup>3</sup> and p<sup>4</sup> are three-rooted and broad. P<sup>3</sup> consists of a stout protocone and a broad postero-internal cingulum expanded and hollowed out posteriorly to form a basin-shaped heel; the anterior and external cingula are reduced or absent. P<sup>4</sup> has a well-developed deuterocone and a larger or smaller tritocone closely joined to the protocone; there is a broad posterior and a narrower anterior cingulum; a crest runs forwards and outwards from the deuterocone to meet the anterior cingulum in front of the protocone.

The deciduous first and second molars are of the same type as their successors. No unworn or unbroken dm<sup>3</sup> is preserved, but it is a three-rooted tooth like its successor, with the protocone over the anterior root; it differs from its successor, however, in being longer in proportion to its breadth and in bearing two cusps over its posterior roots instead of a basin-shaped heel; a narrow basal cingulum is present on all the sides which are unbroken. Dm<sup>4</sup> is four-rooted and quadricuspid, very closely simulating the molars behind it but somewhat smaller; intermediate cuspules simulating proto- and metaconule are present; there is a basal cingulum, interrupted lingually.

M<sup>1</sup> and m<sup>2</sup> are of the conventional bunodont sexi-tubercular type, with two main outer and two main inner cusps, two intermediate cuspules, broad anterior and posterior cingula, a narrow external and no internal cingulum. The posterior cingulum bears a larger or smaller tubercle in the mid-line; other smaller styles are frequently present and the cingula are mammilated. M<sup>3</sup> is referable to this same type, with the addition of a varying number of accessory cuspules and styles which vary also in size and position; the posterior cingulum is very broad, usually forming a prominent heel.

A study of from thirty to forty skulls of recent peccaries of the Colombian species *Tayassu pecari* and of *Tayassu pecari beebei* from British Guiana (for access to which I am indebted to the kindness of the Department of Mammalogy of the American Museum) shows that



even within the same subspecies the molar styles may be very variable; they show every gradation from well-developed cuspules into the usual mammilations of the cingulum; they may even differ in the opposite molars of the same individual. This is especially true of the third molar, and in this tooth the accessory intermediate cuspules also grade from well-developed tubercles into mere ridges on the sides of the main cusps, varying in number and position. In *T. pecari beebei* the two main posterior cusps are usually contiguous at their bases, but the two intermediate cuspules at the anterior end of the valley between them extend back into this valley to a varying extent and may even just touch the tubercle on the cingulum at the posterior end of it. In *T. pecari* these two main posterior cusps may be hardly more separated than in the subspecies or the intermediate cuspules may interpose between them entirely and have a broad contact with the posterior tubercle. These details as to individual variations in recent peccaries are of interest because almost exactly similar variations are found in the third molars of the different genera of fossil forms, and within the genus *Perchærus* itself. It would seem that they cannot be used in making specific distinctions, and it also makes it almost impossible to establish homologies between the cuspules and styles of the different specimens, or between those of the third molar and those of the more conservative first and second molars.

*Helohyus* Marsh has been mentioned as a possible ancestor for the American Oligocene suillines; (Scott, W. B., 1913, 'Land Mammals of the Western Hemisphere,' pp. 273, 361-365; Matthew, W. D., 1915, 'Climate and Evolution,' Ann. N. Y. Acad. Sci., XXIV, p. 242). This small Bridger artiodactyl has been described by Sinclair and referred by him to the Dichobunidæ (1914, Bull. Amer. Mus. Nat. Hist., XXXIII). The skull-back, A. M. N. H. No. 13079, since it comes from one of the lower Bridger formations (B 5), and also on account of its size, even if it is correctly referred to this genus, must have been associated with molar teeth of a type at least as primitive as those of the species *H. plicodon*, so that we would expect to find only the most general indications of suilline ancestry in the skull. What we do find is a structure so primitive and generalized that it is distinguishable in detail only from that of contemporary carnivores<sup>1</sup> and must have been separated by many intermediate stages from the first true suillines such as *Perchærus*, if these are really to be derived from it.

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<sup>1</sup>*Helohyus* is distinguished by the stronger paroccipital process, the much larger post-glenoid foramen, the broader glenoid surface of the squamosal and a post-glenoid process which does not curve forwards over the latter to the same extent as in Carnivora.



The upper molars of *Helohyus*, and what is preserved of the premolars, are again very much more primitive, but at the same time point very strongly towards the *Perchærus* type (Fig. 15). The hypocone is reduced and the metaconule enlarged to take its place—less so in the Bridger (B 3) *H. plicodon*, more so in the Bridger (C 5) *H. milleri*, which is also larger—suggesting the commencement of the process by which, according to Stehlin, all modern Artiodactyl groups have attained a quadrituberculate molar in which the postero-internal cusp is not the hypocone but the metaconule. *Helohyus* further possesses a well-developed protoconule and a small intermediate cuspule, again best developed in *H. milleri*, which bears the same relations to the enlarged metaconule as the latter usually bears to the hypocone, and corresponds in position to the intermediate cusp in the first and second molars of *Perchærus*; this increases the probability of Stehlin's view that the Suidæ, as well as other modern artiodactyls, differ from other mammalian groups in their derivation of a sextitubercular molar from the tritubercular prototype.

The third molar of *Helohyus* lacks the enlarged posterior cingulum of that tooth in *Perchærus* and indeed more nearly approaches the tritubercular type than the first two.

In size the molars of *Helohyus milleri* are quite comparable with those of the smallest species of *Perchærus* I have seen, No. 10510 in the Princeton Museum, from the White River Oreodon Beds of South Dakota. In proportions they differ considerably, for in *Helohyus* the transverse diameter of the upper molars considerably exceeds the antero-posterior, whereas in *Perchærus* the reverse is always true of the third molar and to a lesser extent of the second molar, while the first molar varies.

|                                                      | <i>P. probus</i> Leidy<br>A. M. N. H.<br>No. 1282 | <i>Perchærus</i><br>Princeton<br>No. 10510 | <i>Helohyus milleri</i><br>Sinclair, A. M.<br>N. H. No. 12151 |
|------------------------------------------------------|---------------------------------------------------|--------------------------------------------|---------------------------------------------------------------|
| Length of m <sup>1</sup> to m <sup>3</sup> inclusive | 41.0 mm.                                          | 33.0 mm.                                   | 30.0 mm.                                                      |
| Antero-posterior diameter of m <sup>3</sup>          | 15.5                                              | 10.0                                       | 10.0                                                          |
| Transverse diameter of m <sup>3</sup>                | 13.0                                              | 7.5                                        | 14.5                                                          |
| Antero-posterior diameter of m <sup>2</sup>          | 14.0                                              | 11.8                                       | 10.0                                                          |
| Transverse diameter of m <sup>2</sup>                | 13.5                                              | 8.8                                        | 13.5                                                          |

The fourth premolar of *Helohyus* is very comparable with that of *Perchærus*, but there is apparently no trace of a tritocone and the anterior and posterior cingula are not so broad in comparison with the rest of the



tooth; *Helohyus* further possesses a small intermediate cuspule, lacking in *Perchærus*, on the ridge which leads outwards and downwards from the deuterocone to the anterior cingulum.

There is in the American Museum no sufficiently unbattered third premolar certainly referable to *Helohyus* to make a comparison of value.

#### LOWER JAW

There are no complete, well-preserved lower jaws in the American Museum collection. The fragments show that the symphysis was not so long as in recent peccaries and it sloped upwards at a steeper angle to the inferior border of the ramus.

There are three lower incisors, again fully preserved in *P. trichænus* No. 7390 (Fig. 14) alone. The stumps and alveoli in other specimens show that they tend to be very crowded upon each other and on the canine. (Cook, in the *Pan-American Geologist*, June, 1922, describes an extreme case of crowding in a jaw named by him *Perchærus minor*, from the lowermost clays of the Chadron formation.) As in all suillines, the three incisors are worn on their posterior faces and the first two, which are larger and more procumbent than the third, across the tips as well.

The canine is slightly recurved, has a flat posterior surface where it slides against the upper canine, and bears a ridge on its buccal surface.

P<sub>1</sub> is a small, laterally-compressed cone, usually single-rooted. P<sub>2</sub> is two-rooted, also simple, trenchant and compressed, with a posterior cingulum forming a small heel. P<sub>3</sub> is similar to P<sub>2</sub> but larger and with a better developed heel. In P<sub>4</sub> a deuterocoid is developed, equal in size and slightly posterior to the protoconid from which it is separated by a shallow valley between their tips alone, the posterior heel is extensive and supports a well-developed basal cusp; there is also a smaller anterior basal cusp.

I am indebted to Dr. Milo Hellman for directing my attention to an interesting condition in the occlusion relationships of the deciduous molars in recent Suidæ. In all recent suillines, both New World and Old World, the fourth deciduous molar is an unusual tooth. It resembles a third permanent molar, being very long and possessing three transverse ridges, each composed of two main cusps. From the occlusion of these cusps with the upper molars, however, it would appear that it is the central pair which correspond to a protoconid and metaconid, whereas the anterior pair are a new acquisition, arising, as it were, from an anterior talonid. These two anterior cusps bite into the transverse valley of the almost molariform dm<sup>3</sup>, and the transverse valley between



these two cusps and the central pair receives the posterior pair of cusps of that tooth. The two new cusps thus functionally replace a hypoconid and entoconid on  $dm_3$ , which has only a small cusplike heel and is thus far less molariform than  $dm^3$ .

Of *Perchærus* I have only been able to find a very fragmentary lower jaw still retaining the milk molars (A. M. N. H. No. 1285, from the White River *Protoceras* Beds). Its  $dm_4$  is split but it still shows that already in the Oligocene this tooth was of the six-cusped type described above.  $Dm_3$  has only one main cusp with a deep dint on its posterior surface and even less heel than in recent peccaries.

$M_1$  and  $m_2$  are rectangular teeth with four main cusps of approximately equal size and a small hypoconulid on the posterior cingulum, closing behind the valley between hypoconid and entoconid; the tips of the latter are at a slightly lower level than those of the protoconid and metaconid; there is a narrow anterior cingulum and a discontinuous external cingulum.

$M_3$  has a very broad heel bearing one main cusp or ridge, or a variable number of smaller ones. The same remarks applied to  $m^3$  as to the variability of these small cusps and their relations to the mammilations on the cingulum, and to the lobules on the sides of the main cusps, apply also to  $m_3$ .

The lower dentition of *Helohyus* again affords a good ancestral type but is considerably more primitive in the possession of a simple  $pm_4$  with no deutoconid, of a small paraconid in the molars, and of a much narrower heel to  $m_3$ . No  $m_3$  of *H. milleri*, the species with the most advanced upper molars, is preserved, but the single tooth, A. M. N. H. No. 12150, from the Bridger horizon D 3, doubtfully referred to *H. lentus* Marsh, (see Sinclair, *loc. cit.*, p. 283, Fig. 17) is larger than the corresponding tooth in *P. probus*, A. M. N. H. No. 1283, and considerably larger than some of the smaller species of *Perchærus* (Fig. 16). Indeed, it is its smaller heel alone which prevents it from being entirely comparable in size and proportions with the larger species of that genus, such as *P. pristinus* from the John Day and some of the miscellaneous White River teeth in the collection. Its antero-posterior diameter is 1.93, its breadth at the anterior transverse valley 1.0. In spite of its smaller size the heel bears several small tubercles in addition to the hypoconulid in a manner very similar to that in *Perchærus*; there is a small tubercle on the postero-internal slope of the hypoconid very similar to the ridge or tubercle in several unworn teeth of that genus; the paraconid is reduced to a minute excrescence on the anterior slope of the metaconid.



## YOUNG AND PRIMITIVE CHARACTERS IN THE DICOTYLIDÆ

Three of the skulls in the American Museum collection are those of young animals still retaining their milk dentition. Since two of these young skulls are the only skulls from the White River formation (*Protoceras* beds) whereas the third, from the John Day (*Diceratherium* beds), is at a slightly older stage, it was necessary to determine whether any of the more primitive characters which they showed were due, not to youth alone, but to their being in an earlier stage of evolution. The study in this connection of a very good age series of recent peccary skulls kindly lent me by the Department of Mammalogy brought out the following growth changes in these animals.

1.—Increase in size. There is no evidence of a progressive increase in size in post-Eocene suillines. Even in the Bridger we have seen that *Helohyus lentus* was comparable in size with the larger species of *Perchærus*. The range of size in *Perchærus* skulls is very similar to that in the living genera *Tayassu* and *Pecari*.

2.—Development of well-defined temporal ridges, the brain-case in very young peccaries being smooth and rounded. The three young *Perchærus* skulls already show these ridges well-developed. They unite to form a median sagittal crest as in *Pecari*, but much farther forward than in that genus.

3.—Deepening of lateral depression on snout for the maxillo-labial (*levator labii*) muscles. None of the *Perchærus* skulls, young or adult, show any indication of this depression. (It is present, though very much less marked than in *Tayassu* or *Pecari*, in the Rosebud genus *Desmathyus*.)

4.—Backward passage of the infraorbital foramen in relation to the cheek teeth.

5.—Backward extension of palate behind the tuberosity of the alveolar portion of the maxilla, and correlated changes in the pterygoid region of the alisphenoid. The true appearance of the posterior end of the palate in the fossil skulls is difficult to determine, owing to the bad preservation of this region. It appears, however, to extend back little, if at all, behind the alveolar tuberosity.

6.—Forward shifting of the posterior palatine foramina to a position in front of the canines. This is effected by a closing in of the grooves which lead forwards from the original foramina along the surface of the palate. The closure is, however, imperfect, and leaves sundry minute foramina scattered along its course; these are presumably for branch vessels from the now enclosed posterior palatine artery to the



mucous membrane of the palate. (Stehlin, 'Geschichte des Suiden-Gebisses,' 1899, p. 412, refers to this character.) In *Perchærus* (and *Desmathyus*) the posterior palatine foramina are in their usual posterior position. In the young skulls they are, if anything, farther forward than in the adult (e.g. opposite  $dm^4$  instead of  $m^1$ ).

7.—Formation of a groove in front of the upper canines for reception of the lower. This groove is well-developed in the adult John Day *Perchærus rostratus*, No. 7395, less well in the John Day *P. pristinus*, No. 7394, and still less well in the only fragment of upper jaw of an adult from the White River (*P. probus*, No. 1282). In the young skulls it is barely indicated.

8.—Increase in extent of orbital exposure of the ethmoid. This comes to project beneath the eye as a marked swelling filled with waferous bony tissue. In *Perchærus* this swelling of the ethmoidal region appears to be lacking, but all the skulls are much crushed within the orbit.

9.—Loss of individuality of the very small lachrymal bulla of very young forms as the surrounding parts increase in size. In *Perchærus* the lachrymal bulla is badly crushed in all the young skulls but it is a distinctive feature of the adult John Day forms.

10.—Carrying down of the glenoid surface of the squamosal to a level considerably below that of the basis cranii. This process continues until the tympanic bullæ are nearly hidden in lateral view by the zygomatic wing of the squamosal. This down-carrying takes place in *Perchærus* but to a very much smaller extent.

11.—Development of a more concave glenoid surface, owing to the uprising of a preglenoid ridge. Greater accentuation of the post-glenoid process of the squamosal, which comes to project down beyond the post-tympanic process. In *Perchærus* the glenoid surface remains much flatter and the post-glenoid process projects very little below the post-tympanic.

12.—Lengthening of the tubular external auditory meatus and heightening of the folds of the squamosal which ensheath it. The zygomatic wing of the squamosal comes to extend up as far as the parieto-squamosal suture. The meatus remains comparatively short in the adult *Perchærus*, as in the very young peccary, and the zygomatic wing remains comparatively low.

13.—More marked accentuation of the triangular shape of the bulla. The bulla appears to be larger both actually and proportionally in the young White River skulls than in those from the John Day. It is elliptical in contour and not at all triangular.



14. Loss of sutures. The sutures are more pronounced in the young *Perchærus* skulls but are still traceable in the adult.

These comparisons between youth and age in the individual and in the race showed that all the apparently more primitive characters in the White River skulls could equally well be attributed to youth; there were no obvious evolutionary changes between the first and second phases of the Upper Oligocene. They also established certain characters as primitive in the genus *Perchærus* as a whole and, if to these we add others of an obviously primitive nature or which must be accepted as primitive because they are still shared by recent *Suidæ* in the Old World, we obtain the following list.

#### Primitive Characters in *Perchærus*

1.—Brain development small in comparison with that in recent *Suidæ* and *Tayassuidæ*. In correlation with this are found those conditions of the parietal, squamosal, and orbital regions of the cranium which Matthew in his memoir on 'The Carnivora and Insectivora of the Bridger Basin' (1909. Mem. Amer. Mus. Nat. Hist., IX, part 6, p. 132) indicates as primitive in the early stages of evolution of progressive races. To these may probably be added the close approximation of the supra-orbital canals and the meeting of the ex-occipitals above the foramen magnum to the exclusion of the supra-occipital from its dorsal margin.

2.—Absence of depression, or any clearly defined area of origin, for the levator labii muscles. This depression in *Sus* is not so deep as in recent peccaries but extends much further backward and upward towards the rim of the orbit. The muscles in *Perchærus* were probably much less strongly developed, in correlation with a shorter and less mobile snout and with less powerful canines.

3.—Very slight upturning of maxilla above root of upper canine.

4.—Infra-orbital foramen situated relatively far forward in relation to cheek teeth.

5.—Palate not prolonged backward beyond alveolar border of maxilla. Pterygoid wings of alisphenoids correspondingly long; they are not approximated anteriorly as in *Desmathyus* and *Pecari*.

6.—Posterior palatine foramina in their usual position well back between the cheek teeth (so also in *Sus*).

7.—Foramen ovale completely encircled by the alisphenoid bone. (In all recent suillines there is only a spur of the latter projecting between this foramen and the f. lacerum medium, the two being confluent behind.)

8.—Absence of marked ethmoidal swelling in orbit.



Measurements of the Individual Specimens  
(Corrected to the Nearest Half Millimeter)

| Character of Measurements                                                                                         | White River                  |                            |                            | John Day                       |                                |                           |                             |                             |
|-------------------------------------------------------------------------------------------------------------------|------------------------------|----------------------------|----------------------------|--------------------------------|--------------------------------|---------------------------|-----------------------------|-----------------------------|
|                                                                                                                   | <i>P. probus</i><br>No. 1282 | Young <i>P.</i><br>No. 585 | Young <i>P.</i><br>No. 695 | <i>P. pristin.</i><br>No. 7394 | <i>P. trichin.</i><br>No. 7390 | <i>P. ———</i><br>No. 7398 | Young <i>P.</i><br>No. 7396 | <i>P. rost.</i><br>No. 7395 |
| Total length of skull from back of basi-occipital to tips of premaxillæ.....                                      | .....                        | c. 197                     | .....                      | 229                            | .....                          | .....                     | c. 190                      | 255                         |
| Slant length of snout from edge of lachrymal foramen just below tubercle to anterior extremity of premaxilla..... | .....                        | .....                      | .....                      | 143                            | .....                          | .....                     | 120<br>(v. approx.)         | 173                         |
| Width of skull at posterior ends of zygomatic level with articular surfaces.....                                  | .....                        | 102                        | .....                      | 115                            | .....                          | .....                     | 95.5                        | 130.5                       |
| Distance between top of foramen magnum and foramen rotundum.....                                                  | .....                        | c. 50                      | .....                      | c. 56                          | .....                          | c. 50<br>(crushed)        | c. 52                       | c. 55                       |
| Length of basis cranii from back of basi-occipital to basisphenoid level with f. rotundum.....                    | .....                        | c. 44                      | .....                      | c. 48                          | .....                          | c. 46                     | c. 44                       | c. 48                       |
| Distance between condylar foramina.....                                                                           | .....                        | 19.5                       | ?16.5                      | 21.5                           | .....                          | 23.5                      | 19.5                        | 24                          |
| Length of tympanic bulla.....                                                                                     | .....                        | 25                         | .....                      | 23                             | .....                          | c. 23                     | ?26                         | 21                          |
| Total length of dental series, measured along mid-line of palate.....                                             | c. 120                       | .....                      | .....                      | 143                            | .....                          | .....                     | .....                       | 152                         |



|                                                                                                                                   |      |             |       |      |              |             |                      |
|-----------------------------------------------------------------------------------------------------------------------------------|------|-------------|-------|------|--------------|-------------|----------------------|
| Width across palate at p <sup>2</sup> (or dm <sup>2</sup> ).....                                                                  | 34   | 28          | ..... | 28.5 | .....        | 29          | c. 28.5              |
| Width across palate at antero-internal roots of first molars.....                                                                 | ?29  | 21.5        | ..... | 26   | .....        | 24          | ?29                  |
| Length between canine and p <sup>3</sup> (or dm <sup>3</sup> ).....                                                               | 22   | 22.5        | 22    | 27   | c. 21        | 21.5        | 37 <sup>1</sup>      |
| Length between canine and m <sup>1</sup> .....                                                                                    | 40.5 | 42          | 43    | 47   | .....        | 43.5        | 55.5 <sup>1</sup>    |
| Length from m <sup>1</sup> to m <sup>3</sup> inclusive.....                                                                       | 41   | .....       | ..... | 48   | 45           | .....       | 43.5                 |
| Distance between canine alveolus and alveolus of anterior root of p <sup>1</sup> (or dm <sup>1</sup> ).....                       | 1.5  | almost none | 1.5   | 3.5  | .....        | almost none | c. 12.0 <sup>1</sup> |
| Distance between p <sup>1</sup> and p <sup>2</sup> (or dm <sup>1</sup> and dm <sup>2</sup> ), measured at borders of alveoli..... | 5.5  | 3           | 3     | 7    | .....        | 5           | 6.5                  |
| Distance between p <sup>2</sup> and p <sup>3</sup> (or dm <sup>2</sup> and dm <sup>3</sup> ), measured at borders of alveoli..... | .5   | c. .5       | c. 1  | 1    | almost none  | almost none | 4.5                  |
| Distance between canine alveolus and alveolus of anterior root of p <sup>2</sup> (or dm <sup>2</sup> ).....                       | 13   | 10.5        | 13    | 17   | (v. approx.) | 12.5        | 24 <sup>1</sup>      |
| Antero-posterior diameter of m <sup>1</sup> .....                                                                                 | 12   | 14.5        | 15    | 13.5 | 13           | 13.5        | 13                   |
| “ “ m <sup>2</sup> .....                                                                                                          | 14   | 15.5        | ..... | 16   | 14.5         | 16          | 14                   |
| “ “ m <sup>3</sup> .....                                                                                                          | 15.5 | .....       | ..... | 17.5 | 16.5         | .....       | 16                   |
| Transverse “ “ m <sup>1</sup> .....                                                                                               | 12   | 14          | 14    | 14   | c. 12        | 12.5        | .....                |
| “ “ m <sup>2</sup> .....                                                                                                          | 13.5 | .....       | ..... | 15   | 12.5         | 13          | .....                |
| “ “ m <sup>3</sup> .....                                                                                                          | 13   | .....       | ..... | 15.5 | 13           | .....       | 12                   |

<sup>1</sup>This length is much increased by the the downgrowth of a sheath of maxilla round the base of the canine.



Indices Deduced from the Table Measurements

| Nature of Index |                                                                                                    | <i>P. probus</i><br>No. 1282 | Young <i>P.</i><br>No. 585 | <i>P. prist.</i><br>No. 7394 | Young <i>P.</i><br>No. 7396 | <i>P. rostrat.</i><br>No. 7395 |
|-----------------|----------------------------------------------------------------------------------------------------|------------------------------|----------------------------|------------------------------|-----------------------------|--------------------------------|
| I               | Ratio of length of molar series to total length of dental series, $\times 100$ ....                | 34                           | .....                      | 34                           | .....                       | 29                             |
| II              | Ratio of length from canine to p <sup>3</sup> to total length of dental series, $\times 100$ ..    | 18                           | .....                      | 19                           | .....                       | 24                             |
| III             | Ratio of slant length of snout to total length of skull, $\times 100$ .....                        | .....                        | .....                      | 62                           | c. 63                       | 68                             |
| IV              | Ratio of length from foramen magnum to f. rotundum to slant length of snout, $\times 100$ .....    | .....                        | .....                      | 39                           | c. 43                       | 32                             |
| V               | Ratio of width of skull at posterior ends of zygomata to total length of skull, $\times 100$ ..... | .....                        | c. 52                      | 50                           | c. 50                       | 51                             |
| VI              | Ratio of length from foramen magnum to f. rotundum to width of skull as above, $\times 100$ .....  | .....                        | c. 49                      | 49                           | 54                          | 42                             |
| VII             | Ratio of width of skull as above to slant length of snout, $\times 100$ .....                      | .....                        | .....                      | 80                           | c. 80                       | 75                             |
| VIII            | Ratio of length from foramen magnum to f. rotundum to length of skull, $\times 100$ .....          | .....                        | c. 25                      | 24                           | c. 27                       | 22                             |
| IX              | Ratio of width across palate at p <sup>2</sup> to total length of dental series, $\times 100$ .    | 28                           | .....                      | 20                           | .....                       | 19                             |

| Specific Reference                           | Period | Formation | Beds | Locality                           |                                         |                            |                                     |
|----------------------------------------------|--------|-----------|------|------------------------------------|-----------------------------------------|----------------------------|-------------------------------------|
| No. 1282 <i>P. probus</i> Leidy <sup>1</sup> | {      | {         | {    | {                                  |                                         |                            |                                     |
| 585 "                                        |        |           |      |                                    | Upper Oligocene—White River—Protoceras. | Cheyenne River, S. Dakota. |                                     |
| 695 "                                        |        |           |      |                                    | 1st phase                               |                            |                                     |
| 7394 <i>P. pristinus</i> Leidy <sup>2</sup>  | {      | {         | {    | {                                  |                                         |                            |                                     |
| 7390 <i>P. trichænus</i> Cope <sup>3</sup>   |        |           |      |                                    |                                         | Diceratherium.             | N. fork, John Day River, Oregon.    |
| 7398                                         |        |           |      |                                    |                                         | ?                          | John Day Valley, Oregon.            |
|                                              | {      | {         | {    | {                                  |                                         |                            |                                     |
|                                              |        |           |      |                                    | Upper Oligocene—John Day                | ?                          | "The Cove," John Day River, Oregon. |
|                                              |        |           |      |                                    | 2nd phase                               |                            |                                     |
| 7396                                         | {      | {         | {    | {                                  |                                         |                            |                                     |
| 7395 <i>P. rostratus</i> Cope <sup>4</sup>   |        |           |      |                                    |                                         | Diceratherium.             | John Day Valley, Oregon.            |
|                                              |        |           | "    | Camp Creek, Crooked River, Oregon. |                                         |                            |                                     |

<sup>1</sup>Leidy, 1869, J. Acad. Nat. Sci. Phil., (2) VII, p. 194.

<sup>2</sup>Leidy, 1873, Rep. U. S. Geolog. Surv. of the Territories, F. V. Hayden, I, p. 216, “*Dicotyles*” *pristinus* Cope, 1888, Proc. Amer. Phil. Soc., XXV, pp. 66 and 70, “*Bothrolabis*” *pristinus* (this skull). Cope and Matthew, 1915, ‘Hitherto Unpublished Plates of Tertiary Mammalia,’ Pl. cixa, figs. 9 and 9a, *Perchærus pristinus*, (this skull).

<sup>3</sup>Cope, 1888, *loc. cit.*, pp. 66 and 74, “*Bothrolabis*” *trichænus* (these jaws). Cope and Matthew, 1915, *loc. cit.*, Pl. cxa, fig. 2, *Perchærus trichænus* (one of these upper jaws).

<sup>4</sup>Cope, 1888, *loc. cit.*, pp. 66 and 77, “*Bothrolabis*” *rostratus* (this skull).



9.—Well-developed facial portion of lachrymal bone.

10.—Lachrymal foramen present under cover of lachrymal protuberance. (*Tayassu* has lost both 9 and 10 but both are retained by *Sus*.)

11.—Glenoid surface of squamosal at a level very little below that of the basis cranii.

12.—Flat glenoid surface directed more from side to side, less antero-posteriorly.

13.—Strongly ridged ventral edge to zygomatic bar of jugal, which comes to an abrupt end just in front of glenoid surface, a condition resembling that in *Sus* more than that in late peccaries.

14.—Comparatively short tubular external auditory meatus; zygomatic wing of squamosal not extending up to parieto-squamosal suture.

15.—Egg-shaped or ovoid tympanic bullæ with a few septa on inner surface but free from the cancellous bony tissue which fills them in later peccaries and in *Sus*.

16.—Retention of sutures.

17.—Retention of third upper incisor (so also in *Sus*). All three incisors subequal in size.

18.—Retention of first upper and lower premolars and absence of long diastemata behind the canines (so also in *Sus*).

19.—Retention of comparatively simple, non-molariform premolars.

#### A CONSIDERATION OF THE ACCOMPANYING TABLE OF MEASUREMENTS, OF THE INDICES DEDUCED FROM IT, AND OF OTHER CHARACTERS

It is impossible to do very much in the way of drawing conclusions from the accompanying measurements. The number of specimens is much too small and within this number corresponding parts are rarely preserved intact. Of moderately intact skulls only two are adult—*Perchærus pristinus*, No. 7394, and *P. rostratus*, No. 7395—and therefore suitable for comparison. Nos. 585 and 695 from the *Protoceras* beds of the White River and No. 7396 from the *Diceratherium* beds of the John Day still retain their milk dentition and their third molars are uncut. They have not attained their adult size and proportions. The only measurements which will not be subject to further change are those of the first and, where cut, the second molars. In the two White River skulls (Fig. 6) these are rather larger than in the palate, No. 1282, from the same beds, together with which they have been referred to the species (*P. probus* Leidy. (See p. 83 for references. The teeth described



by Leidy under this name are intermediate in size between No. 1282 and Nos. 585 and 659.) That the length between the canine and the molar teeth in these two young skulls is already greater than in No. 1282 may be partly in agreement with a similar condition in young *Tayassu* skulls, where the length seems out of proportion to that in adults; in these it is because the canine alveolus has not yet attained its full dimensions.

Thus, owing to the nature of the material, specific characters distinguishing *P. probus* from the John Day species can only be sought for in the palate and dentition. The most noticeable points are: the short snout, as indicated by the total length of the upper dental series being more than 2 cms. less than that of *P. pristinus*, whereas Index I is the

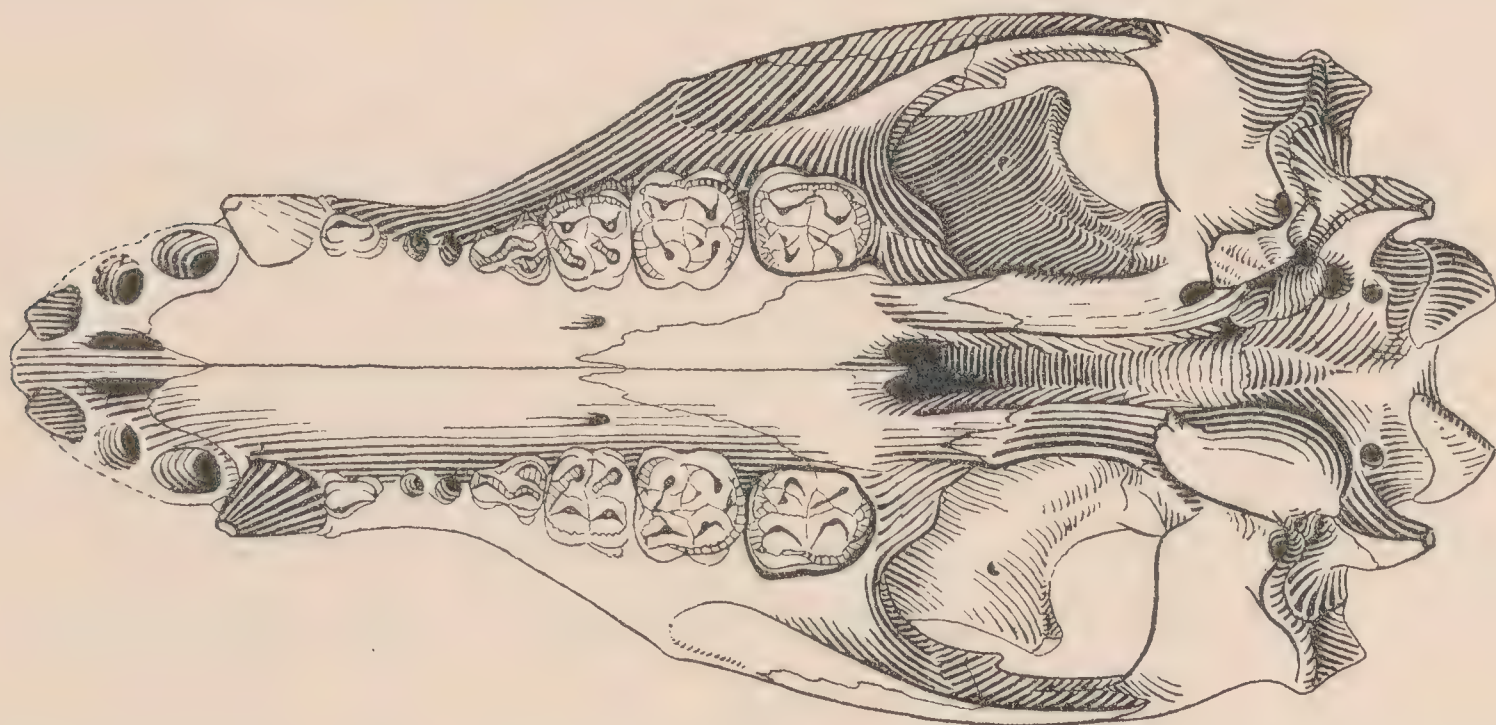


Fig. 6. Reconstruction of the young White River skulls, Nos. 585 and 695.

One-half natural size.

same; the breadth of palate as brought out by the palate measurements and Index IX (these measurements are not wholly reliable, however, as the palate has been broken and plastered); the slight upturning of the maxillary border in front of the canine; and the narrow posterior cingulum to  $m^3$ , this tooth lacking the definite heel of some of the John Day forms.

Sinclair (1905, *loc. cit.*) in differentiating his species lays considerable stress on the spacing of the premolars. This is evidently in a highly variable condition within the genus. It again is a character influenced by age, but in all the American Museum specimens except *P. rostratus*  $p^1$  (or  $dm^1$ ) is very close to the canine and slightly mesial to it. In *P. rostratus* the apparently wide gap between them is largely due to the excessive downgrowth of the maxilla to form a sheath around the base of the canine, possibly for strengthening a longer tooth. *P. rostratus*



is further distinguished by having a much more pronounced diastema between  $p^2$  and  $p^3$ , where as in *P. pristinus* it is only slightly wider than in *P. probus*. In the diastema between  $p^1$  and  $p^2$  all three species much more nearly approach each other, though in *P. rostratus*, considering the length of its snout, it is short when contrasted with that in *P. pristinus*. An indication of the comparative length occupied by diastemata behind the canine in these three species is given by Index II.

No. 7396 (Figs. 7, 8, and 9) has little but youth to distinguish it from the *P. pristinus* type. Indices III, V, and VII show that, although smaller in absolute size, in proportions of length and breadth of skull it already corresponds very closely with *P. pristinus*; the brain-case has

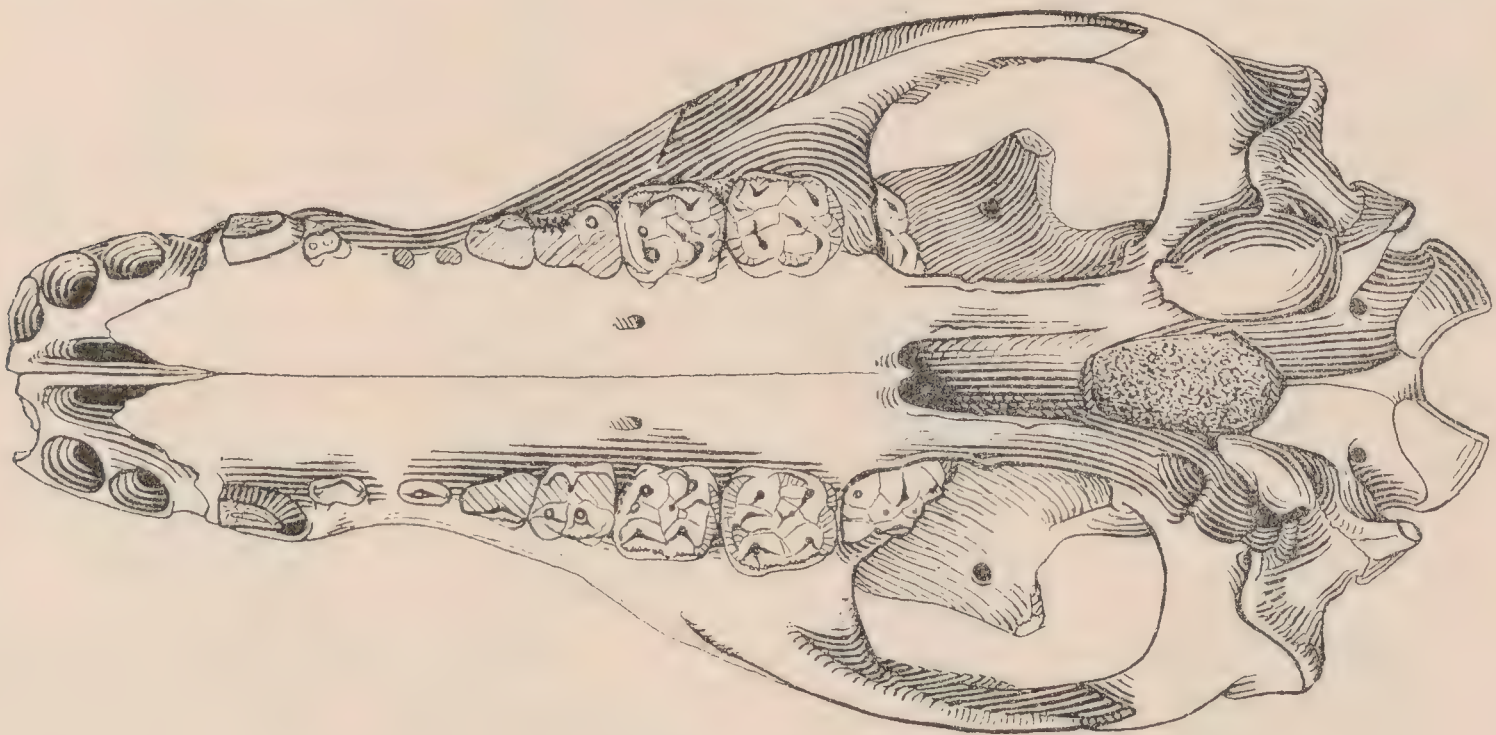


Fig. 7. Young John Day skull, No. 7396.  
One-half natural size.

already attained more nearly adult dimensions, as is brought out by Indices IV and VI. The correspondence between the palatal width at  $p^2$  and that of adult forms is another feature shared by the young *Tayassu*. The antero-posterior diameter of its first two molars corresponds well with those of *P. pristinus*; the transverse diameters are less than in the latter but fall within the 2 mm. range of variation which I found to exist among thirty individuals of the recent species *Tayassu pecari*. (For the antero-posterior diameter of  $m^2$  I found a range of 2 mm. in *Tayassu pecari*, for that of  $m^3$  a range of 4 mm. and for  $m_3$  a range of 6 mm. Though I regrettably had not the time to employ any but the roughest methods of determining these ranges, they were not based on the conditions in rare extremes.) With the pattern of  $m^1$  and  $m^2$  of *P. pristinus* no comparison is possible, for those teeth are quite worn down.



No. 7398 (Fig. 3) consists of a skull-back alone. It closely approaches *P. pristinus* (No. 7394) from which it differs chiefly in the better preservation of its structural details. The difference in the shape of the occipital condyles which comes out in the drawings is probably largely an unreal one, since the ratio of plaster to bone in the condyles of the *P. pristinus* skull is large but not easy to indicate. The ridges for the longi capitis muscles are unusually prominent, especially at their posterior ends,

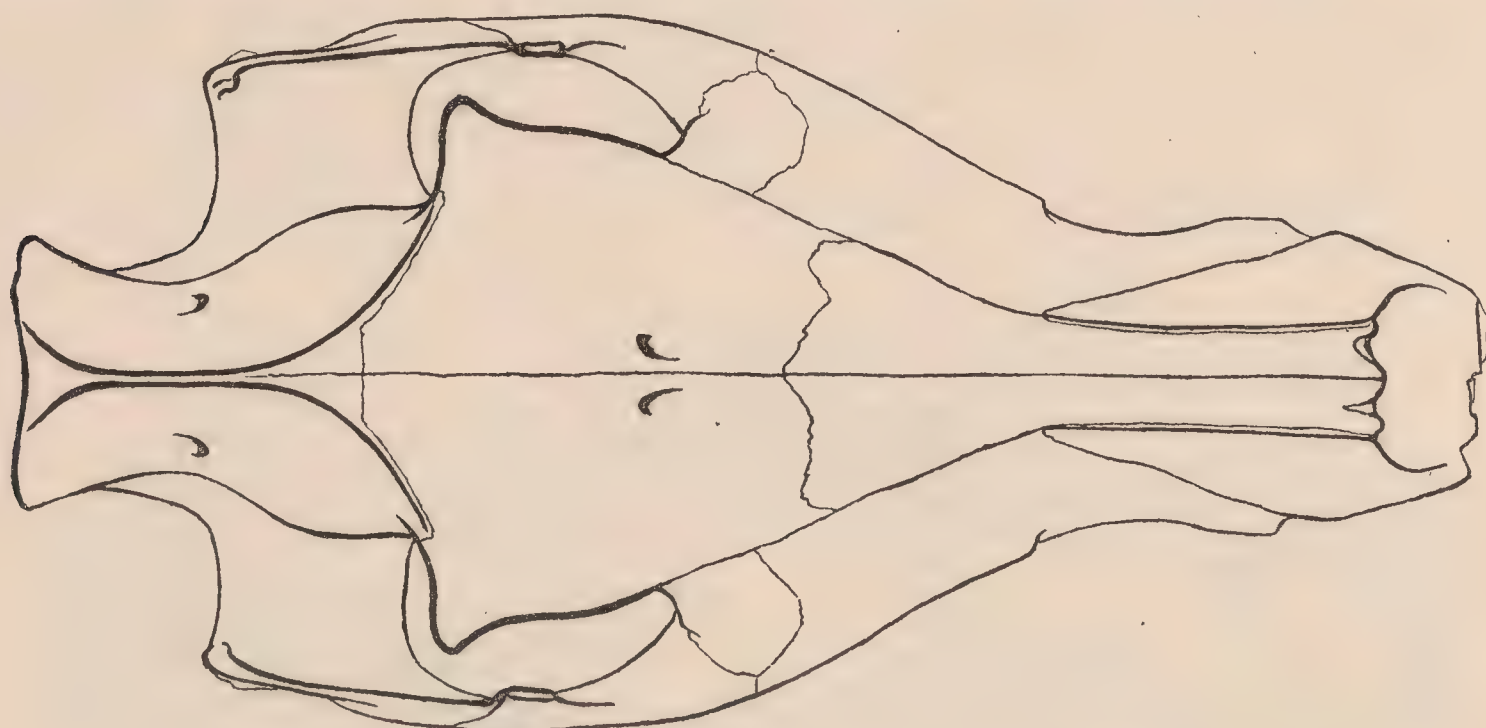


Fig. 8. Young John Day skull, No. 7396.  
One-half natural size.

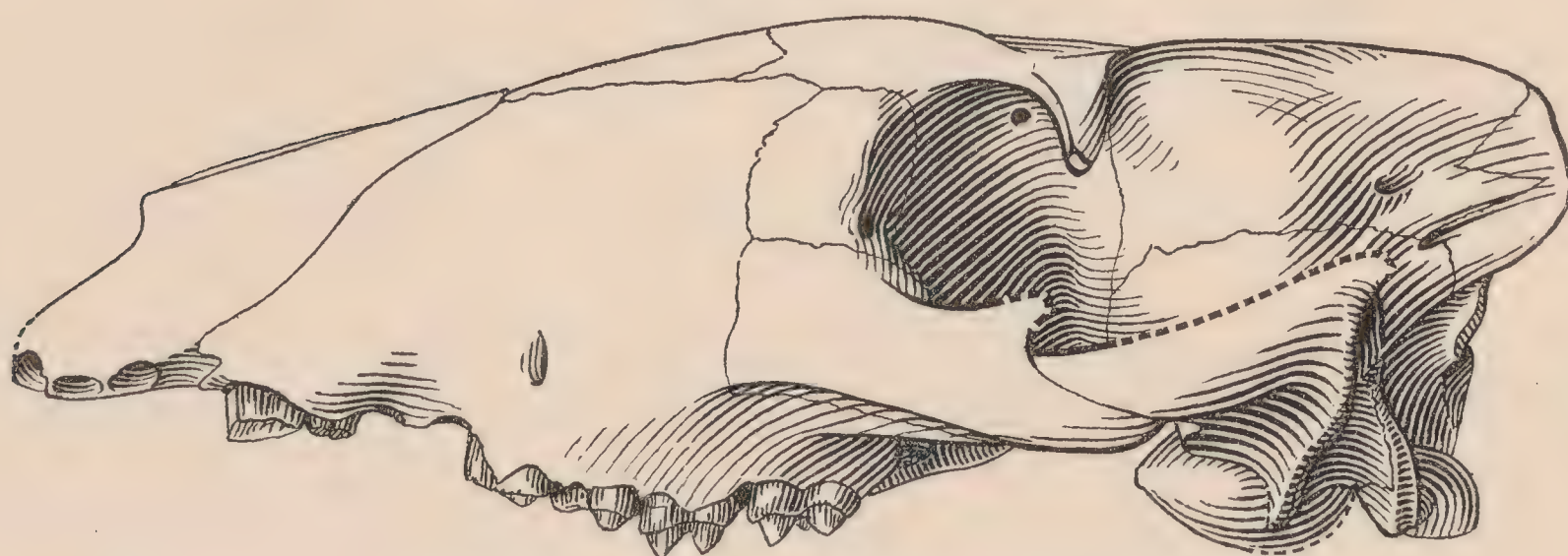
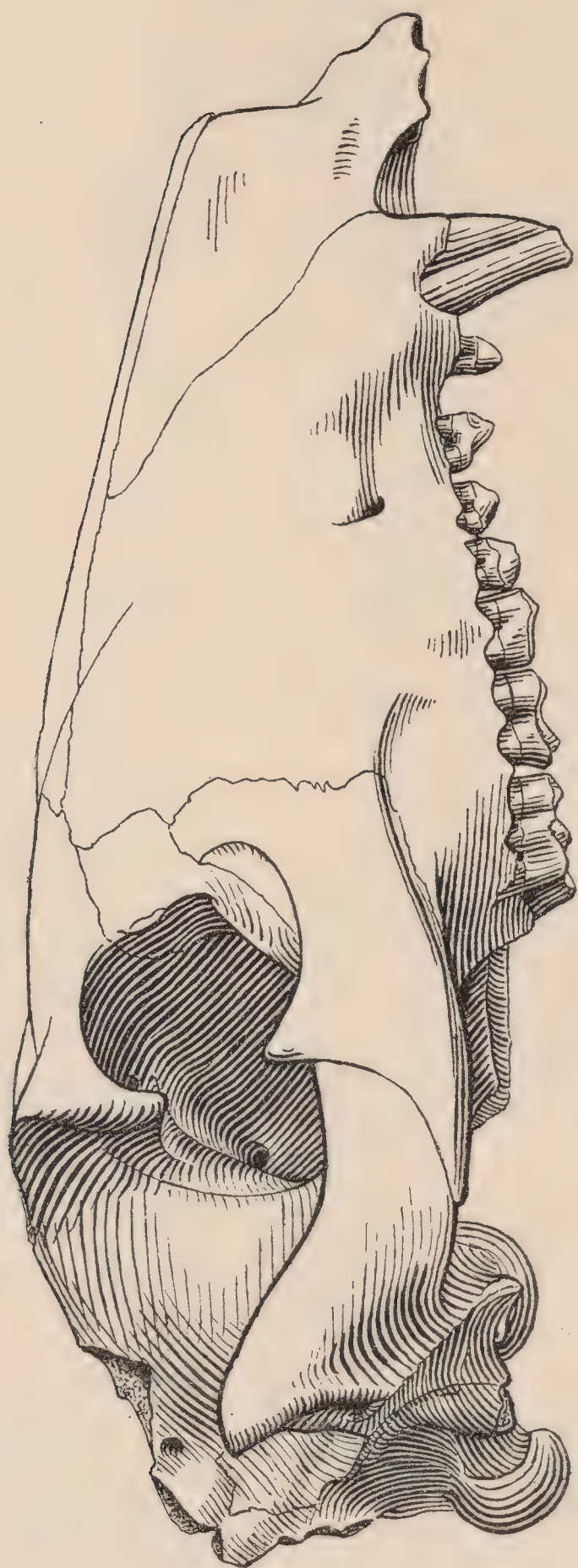


Fig. 9. Young John Day skull, No. 7396.  
One-half natural size.

but very little stress can be laid on this for, as mentioned above, it is a character which varies very greatly within a single species of modern peccary.

*P. pristinus*, No. 7394 (Figs. 10 and 12), itself was described by Cope in 1888 under the generic name "*Bothrolabis*." He distinguished it from the other four species (including "*Chænohyus*" *decedens*) which he described at that time by the characters of the third molar and by the





One-half natural size.

Fig. 10.

Fig. 10. *Perchærus pristinus*, No. 7394.



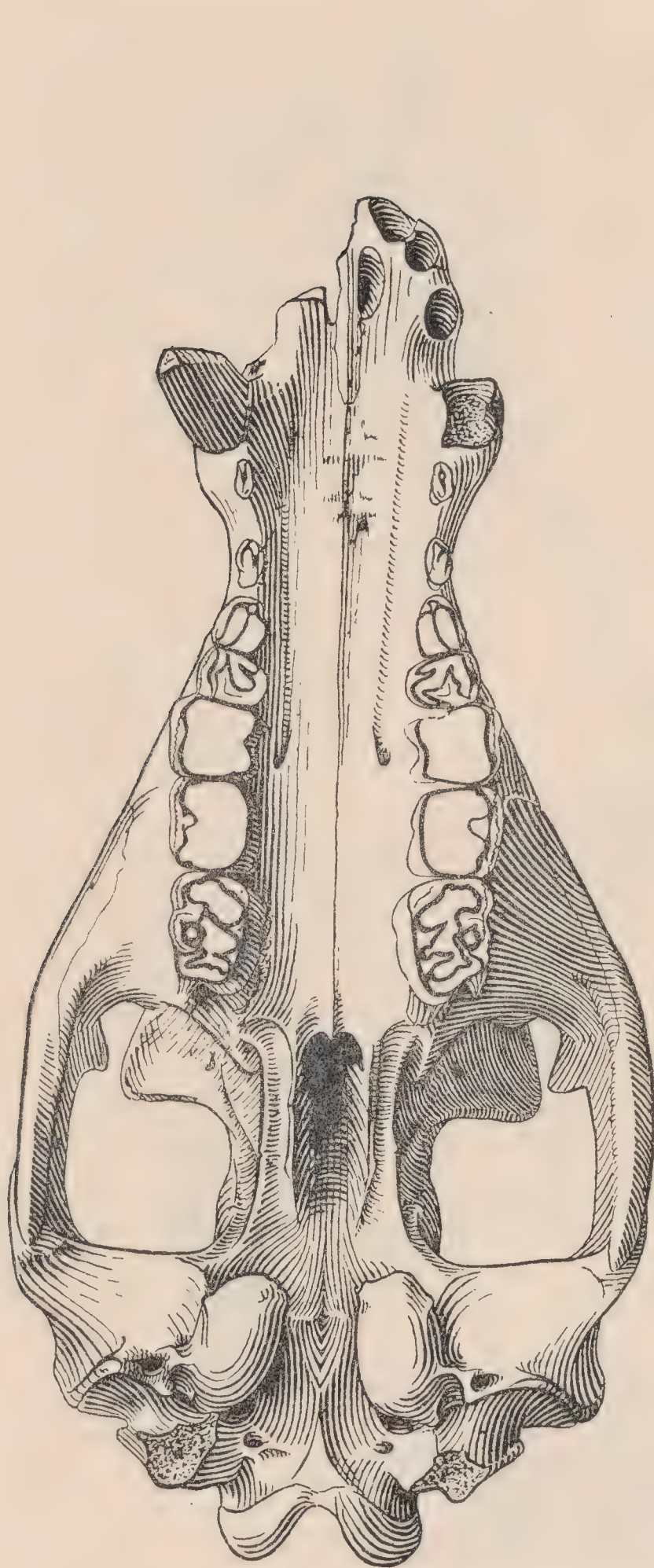
One-half natural size.

Fig. 11.

Fig. 11. *Perchærus rostratus*, No. 7395.

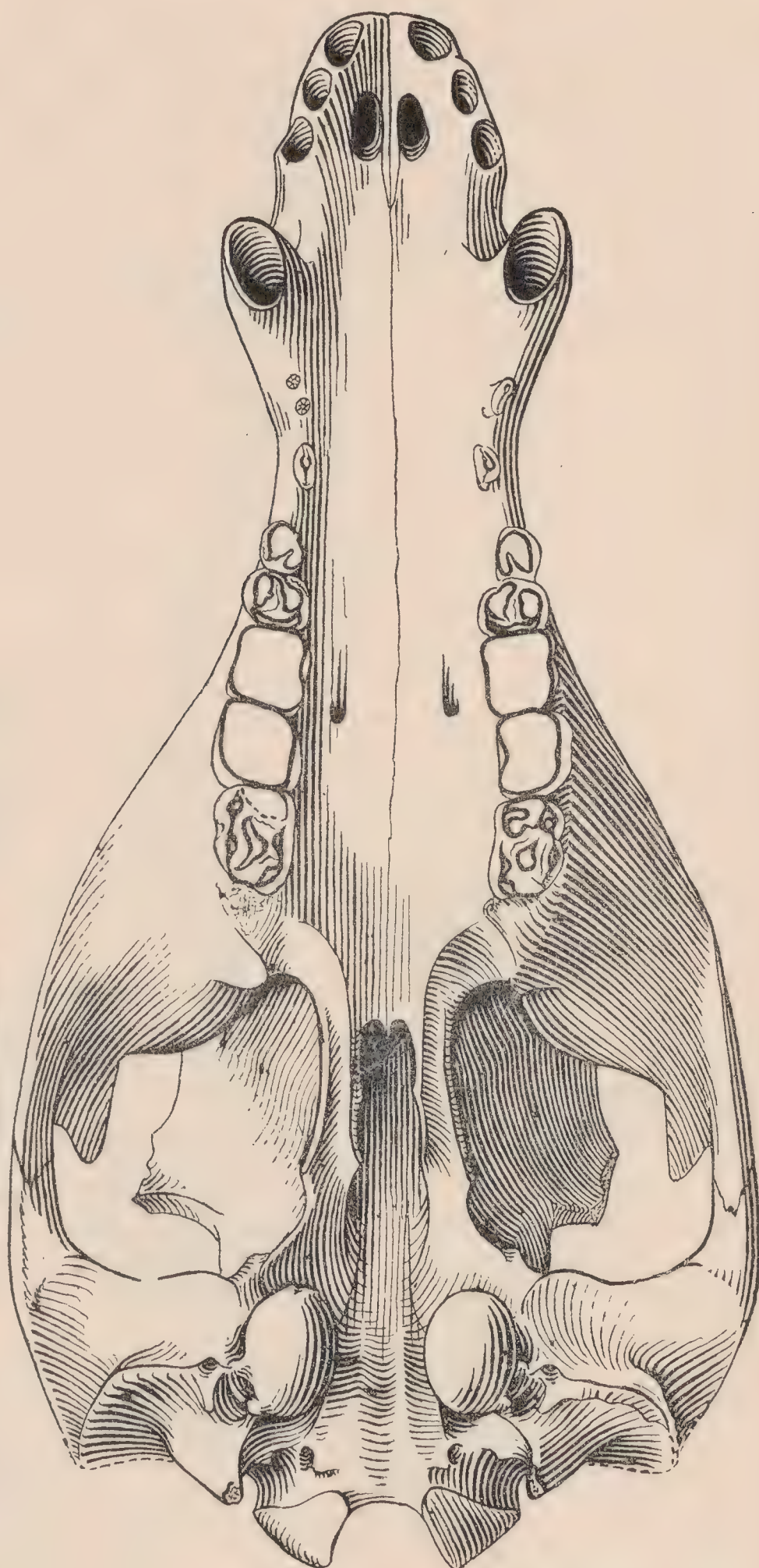
length of the molar series compared with the length from the canine to  $m^1$ . Sinclair (*loc. cit.*, p. 140) in comparing this with other species of "*Thinohyus*" also refers to the character of  $m^3$ . This tooth is considerably worn, the details of its cusp arrangement being lost, but it is char-





One-half natural size.

Fig. 12



One-half natural size.

Fig. 13

Fig. 12. *Perchærus pristinus*, No. 7394.

Fig. 13. *Perchærus rostratus*, No. 7395.

acterized by its very broad posterior cingulum projecting postero-internally as a prominent heel. The comparatively great length of the molar series when contrasted with *P. rostratus* is brought out by Index I. The premolar teeth are also large. The skull is further characterized by



what Cope called a "median frontal rib"—a low ridge in the mid-line of the frontal region of the skull roof behind the supra-orbital foramina; a similar ridge is faintly indicated in No. 7396.

*P. rostratus* Cope, No. 7395 (Figs. 11 and 13), stands out as a distinct type, divergent in size and proportions. It is considerably longer than *P. pristinus*, both in snout and in total length and considerably broader from one zygomatic arch to another. Its basi-occipital is also broader but other measurements of the brain-case are strikingly similar. Indeed, in all the material in which brain-case measurements are possible they are very conservative. Measurements on the outside of the brain-case which will give some idea of the dimensions of the brain are not easy to obtain, but the somewhat approximate ones given of (a) the distance between the top of the foramen magnum and the f. rotundum and (b) the length of the basis cranii from the f. magnum to the basisphenoid level with the f. rotundum are an attempt to approach them, the latter foramen being taken as at the level of the anterior end of the hypophysis and posterior edge of the optic chiasma. Most of the brain-cases are too worn or crushed to make the conventional "greatest width of brain-case" of any comparative value.

That the snout of *P. rostratus* is longer in comparison with the width of the skull at the zygomatic arches than in *P. pristinus* is brought out by Index VII, but that it is at the same time comparatively narrower at the level of  $p^2$  is brought out by Index IX ( $p^2$  is level, or nearly level, with the narrowest part of the snout and palate in all the skulls). The molar teeth are not only comparatively but absolutely very much smaller than in *P. pristinus*;  $m^1$  and  $m^2$  are much worn and much buttressed by plaster and their width and pattern therefore undeterminable;  $m^3$  also has all the smaller details worn away. The spacing of the premolar teeth, which are again smaller than those of *P. pristinus*, and the sheath of maxilla at the base of the canine, have already been referred to. The premaxillæ appear to be bent downwards on the main plane of the palate at a slightly greater angle than in *P. pristinus*; the indentation in front of the upper canine is much deeper; the post-orbital process of the molar is larger; the glenoid surface of the squamosal is carried down to a much lower level with reference to the basis cranii and tympanic bulla. Noticeably distinct from those of all the other skulls are the very small tympanic bullæ, considerably shorter in their absolute length (see table) and apparently without the pointed anterior extremity. Characteristic also is the great antero-posterior breadth of the zygomatic process of the maxilla (compare Fig. 13 with Fig. 12). The palate, though broken



posteriorly, extends back at least as far as the maxillary tuberosity and considerably behind the third molar, whereas in *P. pristinus* it ends considerably in front of the former and only a short distance behind  $m^3$ .

*P. trichænus* Cope, No. 7390, consists of the imperfect jaws alone (Fig. 14). Cope tentatively separated it as a distinct species from *P. pristinus* on account of the smaller molars, the character of  $m^3$  and the possession by  $p_1$  of one root only. Further reference is made to the lower jaw later. The upper molars are certainly considerably smaller than in *P. pristinus* and the prominent postero-internal heel of  $m^3$  in *P. pristinus* and *P. rostratus* is entirely lacking. The molars are narrow in proportion to their length.  $M^3$ , when compared with that of *P. probus*, No. 1282

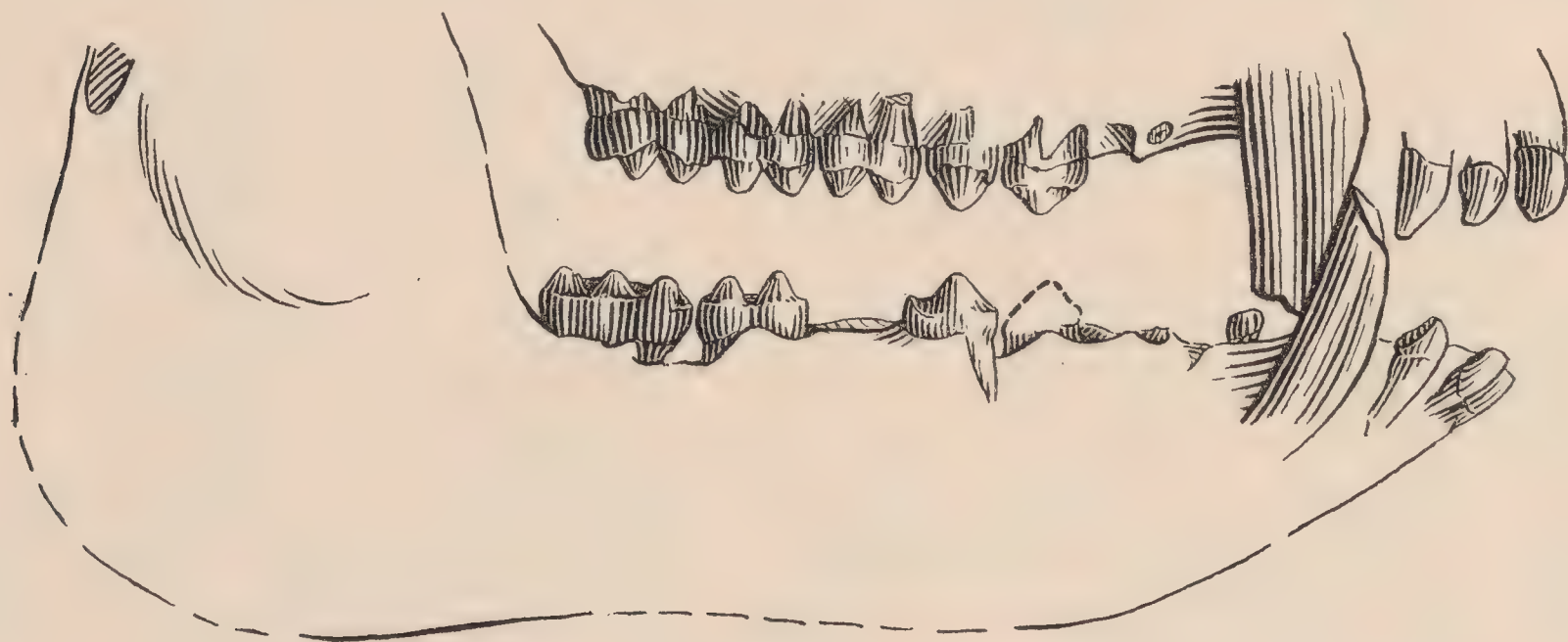


Fig. 14. *Perchærus trichænus*, No. 7390 (partly restored from the opposite side).  
One-half natural size.

(Fig. 15), shows a lack of the large intermediate cusp which in that form separates the two main posterior cusps, unless, indeed, it is the main postero-internal cusp itself which is lacking in *P. trichænus*, as is suggested by the narrow posterior end of the tooth and by the relations of the existing cusp to the cingulum and to the intermediate cuspule in the transverse valley. (See, however, remarks on pp. 72, 73 as to conditions in recent peccaries.) The tritocone on  $p^4$  is very poorly developed and not differentiated from the protocone by a groove on the outer surface of the tooth. The jaw is much battered in the canine region and  $p^1$  and  $p^2$  are lacking on both sides, but the canine appears to have been nearer to  $p^2$  than in any of the other skulls; the alveoli  $p^1$  are not distinguishable, but were probably situated close behind the canine and rather mesial to it, as in the other species.  $I^1$  l.,  $i^2$  and  $i^3$  r. are preserved;  $i^1$  and  $i^2$  are more shovel-shaped and worn on their posterior surfaces,  $i^3$  is more pointed.



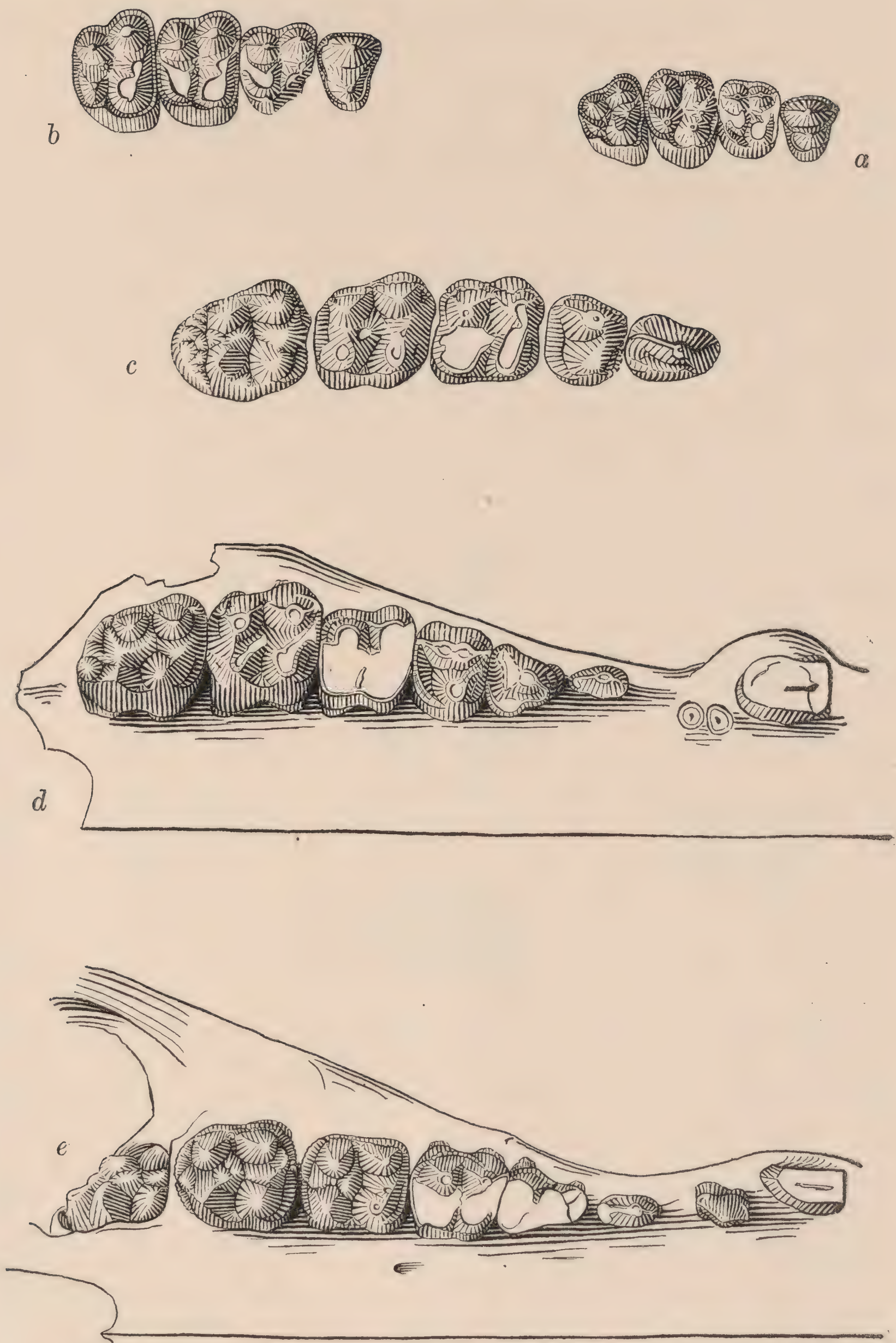


Fig. 15. Right upper dentitions of Bridger and Upper Oligocene suillines (in some cases partly restored from opposite side).

Natural size.

(a) *Helohyus plicodon* No. 12147; (b) *Helohyus milleri*, No. 12151; (c) *Perchærus trichænus*, No. 7390; (d) *Perchærus probus*, No. 1282; (e) *Perchærus* species, No. 7396 (Milk dentition).



Measurements of Lower Jaw Fragments and Teeth  
(Corrected to the Nearest Half Millimeter)

|                                                                            | American Museum Nos. | 12314 | 1283 | 1015B | 1200 | 1286 | ×    | 9812 | 7391 | 7392 | 7390  | 7393 |
|----------------------------------------------------------------------------|----------------------|-------|------|-------|------|------|------|------|------|------|-------|------|
|                                                                            |                      |       |      |       |      |      |      |      |      |      |       |      |
| Depth of mandible below p <sup>3</sup> .....                               |                      | ....  | ?26  | ....  | 26   | .... | .... | .... | 32   | .... | c. 38 | .... |
| Depth of mandible below entoconid of m <sup>3</sup> .....                  |                      | ....  | 28   | ....  | 30.5 | .... | .... | 44   | 30.5 | .... | c. 37 | .... |
| Antero-posterior diameter of m <sub>1</sub> .....                          |                      | ....  | 12   | ....  | 11.5 | .... | .... | 13.5 | 13   | 13   | ....  | 11.5 |
| Antero-posterior diameter of m <sub>2</sub> .....                          |                      | ....  | 13.5 | ....  | 12   | 15   | .... | 15.5 | 14.5 | 15.5 | 15.5  | 12   |
| Antero-posterior diameter of m <sub>3</sub> .....                          |                      | 13.5  | 17   | 23    | 15   | 20.5 | 21.5 | 22.5 | 20.5 | 21   | 21    | .... |
| Length from m <sub>1</sub> to m <sub>3</sub> , inclusive.....              |                      | ....  | 42   | ....  | 38   | .... | .... | 50.5 | 47.5 | 49.5 | ....  | .... |
| Transverse diameter of m <sub>1</sub> .....                                |                      | ....  | 8    | ....  | 8    | .... | .... | 8    | 7.5  | 7.5  | ....  | 7    |
| Transverse diameter of m <sub>2</sub> .....                                |                      | 7.5   | 9.5  | ....  | 9    | 11   | .... | 9.5  | 9    | 10   | 10    | 7.5  |
| Transverse diameter of m <sub>3</sub> (at anterior transverse valley)..... |                      | 7.5   | 8.5  | 12    | 8    | 10.5 | 10   | 11   | 9    | 9.5  | 11    | 8    |
| Breadth of heel of m <sub>3</sub> .....                                    |                      | ....  | 7.5  | 9.5   | 5.5  | 8    | 9    | 9.5  | 8    | 8.5  | 9.5   | .... |

| Specific Reference                       |                                         | Period           | Formation    | Beds                 |  | Locality                    |  |
|------------------------------------------|-----------------------------------------|------------------|--------------|----------------------|--|-----------------------------|--|
| No. 12314.....                           |                                         | Lower Oligocene  | .....        | { Mid. Titanotherium |  | Cheyenne River, S. Dak.     |  |
| 1283 <i>P. probus</i> Leidy <sup>1</sup> |                                         | .....            | .....        | { Mid. Oreodon       |  | Cheyenne River. S. Dak.     |  |
| 1015B                                    |                                         | Middle Oligocene | .....        | { Oreodon            |  | S. Dakota                   |  |
| 1200                                     |                                         | .....            | White River  | { Metamynodon        |  | Cheyenne River, S. Dak.     |  |
| 1286                                     |                                         | .....            | .....        | { Protoceras         |  | Cheyenne River, S. Dak.     |  |
| ×                                        |                                         | Upper Oligocene  | .....        | { "Top"              |  | Crawford, Nebraska          |  |
| 9812                                     |                                         | ?                | ?White River | { ?                  |  | Little White River, S. Dak. |  |
| 7391                                     | <i>P. pristinus</i> Leidy <sup>2</sup>  | .....            | .....        | { Diceratherium      |  | Camp Creek, Crooked River   |  |
| 7392                                     | <i>P. pristinus</i> Leidy <sup>2</sup>  | .....            | .....        | { Diceratherium      |  | John Day Basin              |  |
| 7390                                     | <i>P. trichænus</i> Cope <sup>3</sup>   | Upper Oligocene  | John Day     | { Diceratherium      |  | Camp Creek, Crooked River   |  |
| 7393                                     | ? <i>P. socialis</i> Marsh <sup>4</sup> | 2nd phase        | .....        | { ?                  |  | John Day Basin              |  |
|                                          |                                         | .....            | .....        | { ?                  |  | John Day Valley             |  |
|                                          |                                         | .....            | .....        | { ?                  |  | Camp Creek, Crooked River   |  |
|                                          |                                         | .....            | .....        | { ?                  |  | John Day Basin              |  |

<sup>1</sup>Leidy, 1869, J. Acad. Nat. Sci. Phil., (2) VII, p. 194. ? Marsh, 1894, Amer. J. Sci., XLVIII, p. 271, "*Thinohyus nanus*."  
<sup>2</sup>Leidy, 1873, Rep. U. S. Geolog. Surv. of the Territories, F. V. Hayden, I, p. 216, "*Dicotyles*" *pristinus*. Cope, 1888, Proc. Amer. Phil. Soc., XXV, pp. 66-74, "*Bothrolabis*" *pristinus*. Cope and Matthew, 1915, 'Hitherto unpublished plates of Tertiary Mammalia,' Pl. cxi, fig. 2, *Perchærus pristinus* (jaw, No. 7392).  
<sup>3</sup>Cope, 1888, *loc. cit.*, pp. 66 and 75, "*Bothrolabis*" *trichænus*. Cope and Matthew, 1915, *loc. cit.*, Pl. cxa, *Perchærus trichænus* (upper jaw of this specimen).  
<sup>4</sup>Marsh, 1875 and 1894, Amer. J. Sci. and Arts, IX, p. 249, XLVIII, p. 271, "*Thinohyus*" *socialis*. Cope and Matthew, 1915, *loc. cit.*, Pl. cxi, fig. 3, *Perchærus socialis* (this jaw fragment).



## LOWER JAW FRAGMENTS

Little of importance in species-determination can be added to the accompanying table of measurements; the material is too fragmentary and the teeth in most cases much worn. The table gives some idea of the range of variation, however. It indicates that the animals represented may be divided into two types, a large type and a small type, existing side by side during the Oligocene; the large type was possibly already foreshadowed in the Bridger by *Helohyus lentus* Marsh (see above, p. 76). *Perchærus probus* Leidy, No. 1283, of the White River, forms an intermediate between these two types but more nearly approaches the smaller of them. It is possibly synonymous with "*Thinohyus*" *nanus* Marsh, (1894, Amer. Journ. Sci., XLVIII, p. 271) and the following comparison has been made by O. P. Hay<sup>1</sup>:



Fig. 16. Right third lower molars of Bridges and Upper Oligocene suillines.

Natural size.

(a) *Helohyus validus*, No. 12694; (b) *Helohyus lentus*, No. 12150; (c) *Perchærus probus*, No. 1200; (d) *Perchærus probus*, No. 1283; (e) ? *Perchærus socialis*, No. 7393; (f) *Perchærus trichænus*, No. 7390; (g) *Perchoerus* sp., undetermined, No. 9812.

On making a comparison of this jaw No. 1283 with the type *T. nanus* at Yale the following may be said: No. 1283 is extremely like the type, except that 1283 is larger. The teeth are longer and the width is somewhat disproportionately greater;  $m_1$  is longer and broader;  $m_2$  is longer and broader and especially across its anterior part. The jaw is deeper; under  $m_2$  *T. nanus* 21 mm., No. 1283 28 mm. The latter is possibly a male jaw.

The exact horizon of the Marsh specimen in South Dakota is unknown.

<sup>1</sup>Manuscript note in the American Museum.



To the smaller type belong:

(1.) No. 1200, a jaw fragment with  $p_3$  to  $m_3$ ;  $m_3$  is characterized by a very narrow heel supporting, as in No. 1283, a single main cusp. Compared with the other species the jaw is deep in proportion to the size of the teeth.

(2.) No. 12314, a broken anterior molar and a broken  $m_3$ , each worn and in a broken fragment of jaw; these are the smallest of all the teeth in the collection.

(3.) No. 7393, a jaw fragment with  $p_3$  to  $m_3$ , the latter with its heel broken off. This is the only specimen of the small type from the John Day. The teeth are almost exactly comparable with those of No. 1200 from the White River but not so much worn;  $m_1$  and  $m_2$  are very slightly narrower. It has been assigned by Cope and Matthew (1915, *loc. cit.*) to the species *T. socialis* Marsh, the type specimen of which comes from Oregon, presumably also from the John Day, and consists of two upper molars.

To the larger type belong:

A.—From the White River Formation (for exact horizons, where known, see p. 92).

(1.) No. 9812, a jaw fragment with  $m_1$  to  $m_3$ ;  $m_1$  and  $m_2$  very worn.  $M_3$  has a broad heel with three main cusps and an external cingulum; the antero-buccal of the three cusps is connected with an intermediate cusp or bridge which lies behind and between the entoconid and hypoconid in the posterior transverse valley. The jaw is stout and deep.

(2.) An unnumbered specimen marked X in the table. Part of both rami and the symphysis are present. The alveolar border is much battered and all the teeth except  $m_3$  r. are split and broken off near the roots.  $M_3$  is very much worn; in size it corresponds well with No. 9812; the external cingulum on the heel does not extend to the back of the latter as in that form, and the cusps on the heel appear to have been arranged rather differently.

(3.) No. 1015B, an isolated  $m_3$ , the largest in the collection. The details of its structure are obscured by attrition, but they appear to have been very similar to those in the last two specimens; the trigonid is broader in proportion to the rest of the tooth than in these.

(4.) No. 1284, not included in the table, consists of the symphysial end of a jaw with the broken roots of the incisors, canines and first three premolars of either side, and the worn and broken remains of  $p_4$ — $m_1$  r. In general proportions it is evidently entirely comparable with the last three specimens, though no comparative measurements are possible.



The roots of the incisors, sub-equal in size, are closely crowded on one another and on those of the canines, with only the narrowest alveolar borders between them.  $P_1$  r. has a single root in a large alveolus 4 mm. directly posterior to the canine. No similar alveolus is present on the left side; this appears to be an anomaly or due to an accident rather than an indication of future evolutionary changes. The distance between  $p_1$  r. and  $p_2$  r. is 6.5 mm. The heel of  $p_4$  has an unusually broad cingulum on either side of the central cusp.

(5.) No. 1286, consisting of  $m_3$ , a broken  $m_2$  and the broken symphysis, is slightly smaller than the others of this series from the White River. The roots of its incisors again show crowding, though not quite so extreme as in No. 1284.  $P_1$  is again single-rooted and directly behind the canine but only 2 mm. from it.  $M_3$  is unworn and shows a heel covered with small tubercles instead of supporting two or three larger cusps as in the forms described above. It is closely comparable with  $m_3$  of *P. trichænus*, No. 7390, from the John Day, which is also little worn and with which it agrees in most of those smaller details of tubercle arrangement, so highly variable in recent peccaries, which distinguish the *P. trichænus* molar from that of *P. pristinus*.

*B.*—From the John Day.

(1.) *P. pristinus* Leidy, No. 7392 (Fig. 17), the tooth-bearing portions of two rami connected by a battered symphysis,  $p_3$  r.,  $p_4$  l.,  $m_1$  to  $m_3$  of both sides, and the roots of  $p_2$  r. These may be compared with (2.) *P. pristinus*, No. 7391, a right jaw fragments with  $p_3$  to  $m_3$ , rather worn, and with (3.) *P. trichænus*, No. 7390 (Fig. 14), battered jaws with  $i_1$  to  $c$  of both sides, the stump of  $p_1$  r., a battered  $p_3$  r.,  $p_4$  r. and a broken  $m_2$



Fig. 17. *Perchærus pristinus*, No. 7392. Left Lower dentition,  $p_3$  to  $m_3$ , ( $p_3$  restored from partly broken tooth on right side).

Natural size.

and an  $m_3$  of both sides; the other teeth are mostly represented by roots; it is associated with the upper jaws described above.

These three constitute a very closely connected group, the larger specimen of *P. pristinus* (No. 7392) forming an intermediate link as regards size between the smaller specimen and *P. trichænus*. The jaw of the latter appears to be somewhat deeper and its ventral border to curve down less at the angle than in *P. pristinus*, but this may be in-



fluenced by crush.  $M_3$  of *P. trichænus* is distinguished by the anterior cingulum not curving up into the anterior rib of the metaconid, and by the slightly greater prominence of the intermediate cuspules in the transverse valleys and of the numerous tubercles on the heel.  $M_2$  of *P. trichænus* has a less extensive posterior cingulum than  $m_2$  of No. 7392.  $P_4$  and  $p_3$  are closely similar in both species. In the premolar region of both there are diastemata between  $p_1$  and  $p_2$ ,  $p_2$  and  $p_3$ ; the first of these diastemata measures 7 mm. in *P. trichænus*, the second 4 mm.; in *P. pristinus* the first is not determinable, the second 5.5 mm. According to Cope the jaw of *P. pristinus* in the Condon collection, University of Oregon, has a two-rooted  $p_1$ ; this character is not determinable in the American Museum jaws No. 7391 and 7293; in *P. trichænus*  $p_1$  is single-rooted.

The lower canines of *P. trichænus* have a broad, shallow groove on their lateral surface, separated by a broad rib from a second shallow groove on the antero-buccal surface.  $I_1$  and  $i_2$  are spade-shaped and procumbent, their tips cut off abruptly by wear.  $I_3$  is separated from them at its tip by being less procumbent; the tip is pointed and the crown worn on the edge which faces posteriorly; the tooth corresponds closely in shape with the  $i_3$  of a fragmentary jaw from the Upper Oreodon beds of White River (A. M. N. H. No. 9813), which is probably referable to *P. probus*.



# Article IV.—A CONTRIBUTION TO THE KNOWLEDGE OF *MÆRITHERIUM*

BY H. MATSUMOTO

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## INTRODUCTION

The very important and puzzling genus *Mærittherium* was discovered and described by Dr. C. W. Andrews. He seems to have considered that this genus, as well as *Palæomastodon*, might be on the direct line of ancestry of the Proboscidea and that *Mærittherium* might be ancestral to *Palæomastodon*, as can be judged from his statements as follows:

One long-standing problem, viz., the place of origin of the Proboscidea, may perhaps be regarded as solved already.<sup>1</sup>

Dr. Andrews pointed out the great difference between the Middle Eocene [Qasr-el-Sagha Formation] *Mærittherium* and the Upper Eocene [Fluvio-marine Formation] *Palæomastodon*, and suggested that the more rapid rate at which evolution seemed to have proceeded in the earlier stages of development of many groups of mammals might perhaps in some cases be accounted for as follows:

<sup>1</sup>1901, 'Preliminary note on some recently discovered extinct Vertebrates from Egypt (Part I),' Geol. Mag., Decade 4, VIII, p. 409.



Among the Ungulates, at least, the earlier members of a group are usually of small size, and as specialization advances an increase in bulk also takes place.<sup>1</sup>

Of these genera mentioned above, *Palæomastodon* and *Mæriotherium* appear to be on the direct line of the ancestry of the Elephants and Mastodonts.<sup>2</sup>

Another peculiarity noticed in the remains of *Palæomastodon* is the great variability in the dimensions, even among adult individuals. When it is remembered that this animal is probably the transitional stage between the small *Mæriotherium*, about the size of a tapir, and the large longirostrine mastodonts, this variability in size is particularly interesting as supplying the basis upon which selection could bring about a rapid increase in the dimensions of these early proboscideans, and, indirectly, give rise also to the remarkable series of changes (described elsewhere) which culminated in the production of that characteristic structure in this group, viz., the prehensile trunk.<sup>3</sup>

On the other hand, Dr. Andrews did not overlook the resemblance which exists between *Mæriotherium* and certain earlier sirenians, and observed:

The discovery of an early and comparatively generalized type like *Mæriotherium* naturally raises the question of the relationship of the Proboscidea to other mammals, and although at present it is not possible to arrive at any definite conclusion as to the origin of the group, the view put forward by Blainville and others that they may be related to the Sirenia receives some support.<sup>4</sup>

After the discovery of the fact that *Mæriotherium* occurs also in the Fluvio-marine Formation associated with *Palæomastodon*, Dr. Andrews seems to have become suspicious with regard to *Mæriotherium* being a direct ancestor of *Palæomastodon*, as we see in the following statement of his:

The occurrence of a species of *Mæriotherium*, probably identical with *M. lyonsi*, in the Upper Eocene beds [Fluvio-marine Formation] in association with *Palæomastodon* raises the question of whether *Mæriotherium* can be ancestral to *Palæomastodon*. If it is not, at least it must be extremely similar and very closely related to the actual ancestor, for it presents all the proboscidean characters in exactly the more generalized condition that one would expect to find. Moreover, it may be pointed out that *Palæomastodon* does not occur in the Middle Eocene beds [Qasr-el-Sagha Formation] in which *Mæriotherium* is abundant, while in the upper beds [Fluvio-marine Formation] *Palæomastodon* is common, and but few *Mæriotherium* remains have been found.<sup>5</sup>

In Dr. Andrews' beautiful memoir on the Tertiary Vertebrates of Fayûm, he noticed the following more important characteristics of *Mæriotherium*:

(1) The nasals are short and the nasal opening is not quite at the end of the snout;

<sup>1</sup>On fossil Vertebrates from Upper Egypt,' Proc. Zoöl. Soc. London, 1902, p. 229.

<sup>2</sup>On the evolution of the Proboscidea,' Phil. Transact. Roy. Soc. London, Ser. B., CXCVI.

<sup>3</sup>1903, 'Notes on an expedition to the Fayûm, Egypt, with description of some new Mammals,' Geol. Mag., Decade 4, X, p. 339.

<sup>4</sup>Loc. cit., Phil. Transact., 1903, p. 116.

<sup>5</sup>1906, 'Descriptive Catalogue of the Tertiary Vertebrates of Fayûm, Egypt,' British Museum, p. xvi.



(2) The bones of the back of the skull tend to become swollen by the presence of air cells;

(3) The maxilla send forward on the palate processes which help to support the enlarged second incisors.<sup>1</sup>

As to the life-habits of *Mærittherium*, he observes in the same memoir as follows:

The limbs are unfortunately not well known. The humerus differs considerably from that of the later Proboscidea, but some of the smaller species of *Palæomastodon* from the Upper Eocene [Fluvio-marine Formation] seem to supply intermediate forms; probably the difference arises from the fact that *Mærittherium* was a more or less amphibious type, while the later elephants became fitted for progression on firm ground. The femur approximates very nearly to the form found in the later Proboscidea.

As already mentioned, *Mærittherium* was probably an amphibious, shore, or swamp living animal, and it was no doubt owing to the continuation of the condition favorable to its mode of life that it persisted into the Upper Eocene [Fluvio-marine] period. In the meantime, however, either from this or some closely allied type, there had arisen another more adapted to terrestrial life and showing a great advance in the direction of the typical Proboscidea: to this creature the name *Palæomastodon* has been given.

Subsequently, after the American Museum had secured a splendid collection of mammalian fossils from the Fayûm, Professor Osborn published his own views about *Mærittherium* and *Palæomastodon*, which are partly opposed to those of Dr. Andrews. Several parts of his statement read as follows:

As first announced by Dr. C. W. Andrews, to whom we are chiefly indebted for our present knowledge, *Mærittherium* does anticipate the *Palæomastodon* type in the enlargement of the second pair of upper and lower incisors and in the general pattern of the grinding teeth. Since the wish is always father to the thought, and nothing is more to be desired than a primitive progenitor of the Proboscidea, it was altogether natural to place *Mærittherium* in or near the line of ancestry of the elephant, and in such ancestry, as a member of the Proboscidea, the animal has gone into general literature.

The question of habits and affinity seems so important and interesting that the writer has taken it up afresh with these additional materials. The inquiry was suggested by the general resemblance which the skull of *Mærittherium* bears to that of a sirenian as seen from above and in palatal view. *Mærittherium* not only had no proboscis, but was totally different from *Palæomastodon* both in its appearance and habits, and only very remotely related to this animal, if at all. The study shows, further, that *Mærittherium* is closer to the sirenians and less close to the Proboscidea than has hitherto been supposed.

A profound difference between these animals is brought out in comparing the top and side views of the skull, when it is seen that, whereas the eyes of *Palæomastodon* are in the typical mammalian position above the first permanent grinder, those of

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See footnote above.



*Mærittherium* are very far forward, well raised in the front part of the head, and of very diminutive size, as shown by the shallowness of the sockets. All these are also characters of the sirenian head. As indicated by the auditory meatus the ears are relatively in a more elevated position than in *Palæomastodon*. Both these peculiarities are adaptations to aquatic life to protect the sense organs and bring them near the surface of the water in swimming, so that they will emerge first and disappear last.

Comparison with *Hyrax*, the beaver, and other animals with an enlarged pair of front teeth tends to show that the upper and lower lips were heavy, and fleshy, somewhat similar in form and function, that is, in prehensile power, and that the blunt tusks may have been covered when the mouth was closed, somewhat as in the hippopotami. These tusks were feeding rather than fighting weapons, probably because *Mærittherium* was protected from attack by its aquatic habitat. The conclusion is that *Mærittherium* was a confirmed and continual river-living animal, feeding mainly under water and on the banks, more specialized for aquatic life than the hippopotami, as indicated by its feeble pelvis, but less specialized than the sirenians. It would not be far from the truth to say, from our present knowledge of the animal, that *Mærittherium* is an offshoot of the Proboscideo-Sirenian stock, with *slightly* nearer kinship to the elephants than to the sirenians.<sup>1</sup>

To these views of Professor Osborn, Dr. Andrews made a reply, of which the more important lines read as follows:

As to the characters of the eyes and ears, they seem to be purely adaptive, and are simply the result of the admittedly semi-aquatic habits of *Mærittherium*, and would not be expected to exist in purely terrestrial members of the group. The apparent height of the ears is, moreover, mainly the consequence of the small development of the occipital region of the skull compared with that found in the heavier-headed *Palæomastodon*. As to the arrangement of the jaws and the anterior teeth, it seems to represent exactly such a stage as a mammal with the normal Eutherian dentition would be expected to pass through before attaining the condition found in *Palæomastodon*.

Another argument in favor of the relationship of *Mærittherium* to *Palæomastodon* is the existence of forms like *Mærittherium trigonodon* and *Palæomastodon minor*, which, unfortunately at present are very imperfectly known, appear, both in their size and in some respects in their tooth structure, to be annexed forms.

On the whole, it seems that the weight of evidence is in favor of regarding *Mærittherium* as a proboscidean, though perhaps not on the direct line of ancestry of *Palæomastodon*, and retaining some characters of the original Proboscideo-Sirenian stock.<sup>2</sup>

Professor Schlosser seems to have looked upon *Mærittherium* as rather not an aquatic form, though he appears to have considered it doubtful that it stands on the direct line of ancestry of *Palæomastodon*. Some parts of his statement read as follows:

In seinem Habitus dürfte *Mærittherium* wegen der Länge des Rumpfes, und der niedrigen Extremitäten eher einem Tapir als einem Proboscidier ähnlich gewesen

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<sup>1</sup>1909, 'The feeding habits of *Mærittherium* and *Palæomastodon*,' *Nature*, LXXXI, pp. 139-140.

<sup>2</sup>1909, 'The systematic position of *Mærittherium*,' *Nature*, LXXXI, p. 305.



sein. Auch der Schädel sieht dem von Tapir ähnlicher als dem von *Mastodon*, dagegen verleiht die Länge des Schwanzes mehr das Aussehen eines Raubtieres.

Dass die Gattung *Mæritherium* den direkten Vorfahren *Palæomastodon* darstellt, erscheint einigermaßen zweifelhaft, nicht nur deshalb, weil sie noch mit diesem zusammen gelebt hat, sondern hauptsächlich wegen der nicht geringen Verschiedenheit im Bau des Schädels und wegen der Form ihrer oberen Incisiven, die Backenzähne und allenfalls auch die unteren Incisiven von *Palæomastodon* lassen sich freilich ganz ungezwungen von jenen der Gattung *Mæritherium* ableiten.<sup>1</sup>

Professor Gregory, in his elaborate work on the 'Orders of Mammals,' pointed out several more important characters of *Mæritherium*, classifying them in accordance with the evidence for proboscidean relationship, for sirenian relationship, against proboscidean relationship and for hyracoid relationship, and concluded as follows:

The genus [*Mæritherium*] represents a very primitive offshoot from the Proboscideo-Sirenian stock. Its dentition and certain other characters indicate a nearer alliance with the Proboscidea than with the Sirenia, but it is far more primitive than any other known representative of either order.<sup>2</sup>

Recently, the same author, in his exhaustive study on the lacrymal bone of vertebrates, has expressed the following views:

The orbital region [of *Mæritherium*] is much more primitive than that of other Proboscidea, and suggests the sirenian type.<sup>3</sup>

As to the relations of the *Mæritheriidae*, while it is quite possible that *Mæritherium* is related to the Sirenia (Osborn, 1909) the numerous detailed and peculiar resemblances to *Palæomastodon* in dentition and skull structure fully support Dr. Andrews in regarding it as the most primitive known member of the Proboscidea.

The lacrymal region of Proboscidea (p. 180) is specialized through the forward shifting of the orbits and thus affords no definite evidence of relationship with more primitive groups. The lacrymal region of *Mæritherium* is far more primitive than that of *Palæomastodon* and, in connection with other evidence, it supports the view that *Palæomastodon* was derived from a *Mæritherium*-like stage.

The Sirenia, although very highly specialized for aquatic life, show special resemblances with *Mæritherium* in the skull (including the orbital region) and dentition, and are generally regarded as a derivative of the proboscidean stem.<sup>4</sup>

The more the problem becomes complicated the more a precise revisional study is needed. It may possibly be out of the question, at present, to decide whether *Mæritherium* is proboscidean or not, whether it is an ally of *Palæomastodon* or not, or whether it resembles the earlier sirenians in a certain degree or not at all. Then, the questions we have to face are: (1) in what degree and in what manner, is *Mæritherium* allied with *Palæomastodon* and the other proboscideans; (2) in what

<sup>1</sup>1911, 'Beiträge zur Kenntnis der Oligozänen Landsäugetiere aus dem Fayûm (Egypt),' Beitr. z. Pal. n. Geol. Österreich-Ungarns u. d. Orients, XXIV, pp. 154-155.

<sup>2</sup>1910, 'The Orders of Mammals,' Bull. Amer. Mus. Nat. Hist., XXVII, p. 368.

<sup>3</sup>1920, 'A Review of the Evolution of the Lacrymal Bone of Vertebrates with Special Reference to that of Mammals,' Bull. Amer. Mus. Nat. Hist., XLII, p. 180.

<sup>4</sup>*Loc. cit.*, p. 245.



degree and in what manner, does *Mærittherium* resemble the earlier sirenians, as well as (3) the hyracoids; (4) in what degree and in what manner, does *Mærittherium* differ from the earlier sirenians, as well as (5) from the hyracoids; (6) was *Mærittherium* an aquatic or semi-aquatic form, and in what degree was it so, if at all?

The material of the genus in question secured by the American Museum is fairly rich and splendid, so a precise study of it may, I presume, contribute somewhat to our knowledge of this genus. Professor Henry F. Osborn, President of the American Museum, has generously and kindly submitted to me this material to study.

During this study I have received much kind help and advice from Professor Osborn, Doctor W. D. Matthew, Professor William K. Gregory and Mr. Walter Granger. I have the greatest pleasure in expressing here my hearty thanks to all these gentlemen, as well as to Mrs. L. M. Sterling, who prepared the drawings, and to Mrs. E. M. Fulda, who prepared the photographs in this report.

#### PALÆOBIOLOGY AND PHYLOGENETIC POSITION

##### A.—CHARACTERS POSSIBLY INDICATING AQUATIC ADAPTATION

(1.) The skull, including occiput, is very low, and the upper surface of the skull runs almost evenly from the anterior ends of the nasals to the top of the lambdoid crest. This character, as stated by Andrews and Osborn, might be regarded as an aquatic adaptation. On the other hand, it cannot be regarded as exclusively so, since it might also be a primitive character. We see that *Saghatherium*, *Mixohyrax*, *Geniohyus*, *Pterodon*, *Apterodon*, etc., of the Fluvio-marine Formation of the Fayûm, had also the low and even skull.

(2.) The orbits are rather high and situated very far forward. Their high situation might possibly be, as pointed out by Osborn, a character of aquatic adaptation in certain degree. But, the roofs of the orbits are not flared upwards and the anterior borders of the same do not project outwards, quite unlike the conditions observed in the sirenians and hippopotami.

The anterior situation of the orbits might not be an aquatic adaptation. We see many mammals and reptiles profoundly adapted to an aquatic life with very posteriorly situated orbits. The small size of the orbits might also not be an aquatic adaptation.

(3.) The external nares are retired backwards to a short extent. The retirement of the external nares is either an aquatic adaptation or it is correlated with the possession of a more or less prehensile upper lip



or proboscis. To which of these two adaptations might the said character of *Mæritherium* correspond?

The posterior border of the external nares of *Mæritherium* is not rounded but is indented by the insertion of the anterior parts of the nasals, which show a tendency partly to roof over the external nares. Such a structure is observed also in the other proboscideans, tapirs, *Alces*, *Saiga*, and many other terrestrial mammals, with a more or less prehensile upper lip or proboscis. The backwardly retired external nares of many aquatic mammals and reptiles face upwards and have rounded posterior borders. Judging from these facts, the backwardly retired external nares of *Mæritherium* might very probably correlate with the possession of a more or less prehensile upper lip—a step toward a proboscis—instead of being an aquatic adaptation.

(4.) The external auditory openings are on a high level. As pointed out by Osborn, this character might be an aquatic adaptation in a certain degree. On the other hand, it cannot be regarded so exclusively. We see the fact that the external auditory openings of very many ungulates, such as the amblypods, hyracoids, sirenians, titanotheres, tapirs, rhinoceroses, horses, pigs, elotheres, hippopotami, anthracotheres, oreodonts, camelids, tragulines, cervids, merycodonts, etc., are located on a high plane above the level of the occipital condyles. It is evident that some of these ungulates are aquatic in their habits, but it is also evident that others are not aquatic but thoroughly terrestrial.

On the other hand, the external auditory openings of *Palæomastodon* and *Trilophodon* are higher in their position relative to the occipital condyles than those of *Megabelodon*. Again, those of the short-jawed mastodonts and elephants are very high in their position relative to the occipital condyles. Within the limit of the proboscideans, the external auditory openings are higher in their position relative to the occipital condyles in those forms with a short skull than in those with a long skull; as well as in those forms with the ascending bars of the mandible erect or inclined forward rather than in those with the ascending bars inclined backward.

Thus, the highly placed external auditory openings of *Mæritherium* are a character in common with many groups of ungulates; a primitive character within the limit of the earlier proboscideans; and a character correlated with the short skull, as well as with the erect or forwardly inclined ascending bars of the mandible, within the limit of the Proboscidea as a whole. Consequently, the idea that the said character of *Mæritherium* is an aquatic adaptation must not be over-estimated.



To summarize, *Mærittherium* might not have been adapted very much to an aquatic life. Evidently, it might be less aquatic than hippopotami. Judging, however, from the structure of the cheek-teeth, as well as from the stratigraphical occurrence of the remains of this animal, there can be no doubt that its favorite haunts were watery districts.

B.—CHARACTERS INDICATING TERRESTRIAL AND NON-AQUATIC  
ADAPTATION

(1.) The zygomatic arches lie very low and are not very stout. Those of the sirenians and hippopotami, on the contrary, lie very high, so that the upper surface of the head is very broad and flat, the upper edges of the zygomatic arches showing a tendency to reach nearly the level of the upper surface of the head. Moreover, those of the sirenians, especially, are very stout, being much stouter than those either of *Mærittherium* or of *Palæomastodon*.

(2.) The roofs of the orbits are not flared upwards and the anterior borders of the same do not project outwards, as already stated under A (2).

(3.) The backwardly retired external nares face forwards, instead of facing upwards, with their posterior border not rounded, showing a tendency to be partially roofed over by the anterior parts of the nasals, as already stated under A (3).

(4.) The olfactory lobes of the brain-case cast are very large, a character of non-aquatic mammals as pointed out by Andrews. Those of *Eotherium* and *Eosiren* are exceedingly small, a character of aquatic mammals.

(5.) The lower incisors are very close-set, and form together something like a spade. Such a spade-like arrangement of the lower incisors is also observed in *Palæomastodon*, *Trilophodon*, *Megabelodon*, boars, diprotodonts, etc. The mode of using the mandible with such a spade-like arrangement of the lower incisors may be conceived as being in the mode of the boars. Such an arrangement is an adaptive structure to digging and rooting in a terrestrial life. Moreover, even if we neglect the spade-like arrangement of the lower incisors, their very close setting is observed only among mammals of non-aquatic life. The lower incisors seen in some aquatic mammals are always well-spaced, a structure adapted to digging and rooting in an aquatic life and to seizing objects which float in or on water.

(6.) As far as I have examined the material in the American Museum, the vertebræ are opisthocœlous, instead of being biplanous. This



character is common in terrestrial mammals, in contrast with aquatic mammals.

(7.) The lumbar vertebræ and sacrum are well differentiated, (Andrews) and the latter consists probably of four vertebræ (Schlosser).

(8.) Both the anterior and the posterior limbs are well developed (Andrews).

To summarize, *Mærittherium* might be a terrestrial form quite as stated by Andrews (former opinion) and by Schlosser. The life-habits of *Mærittherium* might be in some ways like those of tapirs and boars.

#### C.—CHARACTERS IN COMMON WITH THE HYRACOIDS

(1.) The skull is very short in comparison with the zygomatic width. This character is common also to some of the hyracoids in striking contrast to the earlier sirenians and even to the earlier proboscideans. *Palæomastodon* is more long-skulled than the present genus but is more short-skulled than *Trilophodon* and *Megabelodon*.

(2.) The skull, as well as the occiput, is very low, its upper surface running almost straight from the anterior ends of the nasals to the lambdoid crest. This character is evidently primitive and is common also to the hyracoids and very earlier sirenians, as already stated under A (1).

(3.) The sagittal crest is well developed along the median line of the parietal region, a character common to this genus, *Palæomastodon*, and many hyracoids, in contrast to the sirenians and other proboscideans.

(4.) The snout is very short and wide. The short snout is a common character of this genus and some of the hyracoids in contrast to the earlier sirenians and earlier proboscideans, while the wide snout is a characteristic of the proboscideans in contrast to both the hyracoids and sirenians.

(5.) The premaxilla and frontal are separated from each other by the maxilla and nasal, which meet to form the naso-maxillary suture. This character is common to this genus and the hyracoids in striking contrast to the sirenians and other proboscideans.

(6.) The roofs of the orbits are not flared upwards and the anterior borders of the same are not projected outwards, a character common to the hyracoids and proboscideans in contrast to the sirenians, as already stated under B (2).

(7.) The antorbital foramina are not extremely large and conspicuous, a character common to the hyracoids and proboscideans in contrast to the sirenians, although those of the hyracoids are very small and very anteriorly situated.



(8.) The outer borders of the snout and zygomatic arches in upper or lower view form together a very smooth continuous curve on either side. This character is common to the hyracoids and earlier proboscideans in contrast to the sirenians.

(9.) The zygomatic arches are set very low and are not very stout. This character is common to the hyracoids and proboscideans in contrast to the sirenians, as already stated under *B* (1).

(10.) The jugals extend from the posterior lower corners of the orbits to back of the glenoid fossæ. This posterior limit of the jugals is a common character of the hyracoids and proboscideans in contrast to the sirenians, although the anterior limit of the same just observed in this genus is quite characteristic of the proboscideans in striking contrast to both hyracoids and sirenians.

(11.) The zygomatic process of each squamosal reaches forward about to the middle of the zygomatic arch behind the orbit. This is a common character of some of the hyracoids and proboscideans. In some other hyracoids it reaches forward only to a considerable distance behind the middle of the post-orbital portion of the arch, and in the sirenians it reaches almost to the postorbital process.

(12.) The upper limit of the squamosals is a considerable distance below the level of the top of the parietal surface, that is not so high as almost to reach the same level. This is a proboscidean character and appears to be common also to some of the hyracoids in contrast to the sirenians and some other hyracoids. In the two last-named groups, the upper limit of the squamosals nearly reaches the level of the top of the parietal surface.

(13.) The external auditory openings are set very high. This character is common to many groups of the ungulates, as already stated under *A* (4). Moreover, those of this genus are placed rather higher even than those of certain sirenians.

(14.) The external auditory meatus is fairly well-closed in lower view, a character common to the proboscideans and hyracoids in striking contrast to the sirenians, though the degree of the closing of the meatus is more advanced in the proboscideans than in the hyracoids.

(15.) The squamosal, supraoccipital and exoccipital are fully in contact, all together, leaving no conspicuous slit between them, so that the periotic is not exposed on the occipital surface at all. This character is common to both the hyracoids and proboscideans in striking contrast to the sirenians.



(16.) The pterygoid processes, each of which is composed of the pterygoid, alisphenoid, and the posterior portion of the palatine, are not exceedingly stout and do not project downwards so far as to reach the level of the grinding surfaces of the upper cheek-teeth. This is a common character of both the hyracoids and proboscideans in striking contrast to the sirenians. In the last-mentioned group, they are exceedingly stout and project downwards as far as below the level of the grinding surfaces of the upper cheek-teeth.

(17.) In one very fine skull of *Mærittherium* belonging to the American Museum, I have noticed that the posterior alisphenoid canals and foramina ovalia are distinct from the nearly confluent openings of the foramen lacerum medium, carotid canal, foramen lacerum posterius, and condylar foramen. The distinctness of the posterior alisphenoid canals and foramina ovalia from the more posteriorly located foramina is a common character of the hyracoids and proboscideans in striking contrast to the sirenians. The confluence of the condylar foramina with the more anteriorly located foramina, however, is a character of the proboscideans, as well as of some individuals of the modern *Manatus*, in striking contrast to the hyracoids and sirenians, except as stated. In the sirenians, the posterior opening of the alisphenoid canal, foramen ovale, foramen lacerum medium, carotid canal, and foramen lacerum posterius of either side are all confluent, forming a large slit, while the condylar foramina are distinct from them, except in some individuals of modern *Manatus* in which these also are confluent with them.

(18.) The paroccipital processes are comparatively thin antero-posteriorly. This is a common character of the hyracoids and proboscideans in contrast to the sirenians.

(19.) The ascending bars of the mandible incline slightly forwards. This is a common character of the hyracoids, the sirenians with the possible exception of *Eotherium* (so far as Abel's restoration<sup>1</sup> of the mandible is correct), and certain short-jawed mastodonts and elephants, in contrast to *Palæomastodon* and the long-jawed mastodonts.

(20.) The mandibular rami do not show a conspicuous downward bending just behind the symphysial region. This is a common character of *Mærittherium* and the hyracoids in contrast to the sirenians and even many earlier proboscideans.

(21.) The symphysis is comparatively short, a character common to this genus, the hyracoids, sirenians, and short-jawed mastodonts and elephants in contrast to *Palæomastodon* and the long-jawed mastodonts.

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<sup>1</sup>1913, 'Die Morphologie der eocänen Sirenen der Mittelmeerregion,' *Palæontogr.*, LIX, p. 349.



(22.) I have noticed in two specimens in the American Museum presenting the symphysial regions of mandibles, that the groove on the upper surface of the symphysis is rather like a depression, being slightly concave antero-posteriorly, besides being strongly concave from side to side. Such a depression is also present as a part of the groove on the upper surface of the symphysis also in *Palæomastodon* and the long-jawed mastodonts. In certain hyracoids, also, such a depression is observed to be present on the upper surface of symphysis. In the sirenians, however, the depression which corresponds to that just mentioned in the hyracoids and proboscideans is present on the upper posterior or posterior surface of the symphysis and is extraordinarily strong, as a characteristic of this group.

(23.) The anterior mental foramina are not very large and conspicuous, a character common to the hyracoids and proboscideans in contrast to the sirenians.

(24.) The full number of the upper incisors and canines is present, as in the earlier hyracoids and earlier sirenians, though their arrangement is different from that in these groups.

(25.) The second lower incisors of both jaws are enlarged and tusk-like, being distinctly larger than the first. In the hyracoids, the second lower incisors are likewise enlarged and tusk-like.

(26.) The cheek-teeth are bunodont showing an inclination to be lophodont, quite like those of some sirenians and some other proboscideans, as well as some hyracoids, though those of these groups differ from each other in detail.

Among these twenty-six characters examined, sixteen, *viz.* (3), (6), (7), (8), (9), (10), (11), (12), (14), (15), (16), (17), (18), (22), (23), and (25), are common to both the hyracoids and proboscideans in contrast to the living or earlier sirenians; four, *viz.* (1), (4), (5), and (20), are common to the present genus and the hyracoids in contrast to the sirenians and proboscideans or earlier forms of them; four, *viz.* (2), (19), (21) and (24), are common to the present genus, the hyracoids, and sirenians in contrast to the other proboscideans; one, *viz.* (13), is common to many primitive groups of ungulates; and one, *viz.* (26), is common to all the hyracoids, sirenians, and older proboscideans. It may easily be seen that *Mærittherium* has many characters common both to the hyracoids and to other proboscideans in contrast to the living or earlier sirenians.



D.—CHARACTERS DISTINCTIVE FROM THE HYRACOIDS

(1.) The mid-cranial region is long, slender, and tubular, a character common to this genus and the earlier sirenians in contrast to the hyracoids, later sirenians, and other proboscideans.

(2.) The snout is wide, a characteristic of proboscideans in contrast to the hyracoids and sirenians, except *Desmostylus*.

(3.) The external nares are situated some distance behind the anterior end of the skull, a character common to the sirenians and proboscideans in contrast to the hyracoids.

(4.) The orbits are situated very far forward, a character common to this genus and the sirenians in contrast to the hyracoids and even other proboscideans.

(5.) In lateral view, the orbit is bordered above by the frontal and anteriorly as well as below by the maxilla, the jugal reaching only as far anteriorly as the lower posterior corner of the orbit. The situation of the lacrymal in this genus is not yet clear, though it is almost certain that no distinct lacrymal is present in front of the orbit; the lacrymal might either be absent or be present deep within the orbit. The condition of the border of the orbit just observed in this genus is a characteristic of the proboscideans, laying aside the problem of the situation of the lacrymal. In the hyracoids the orbit is bordered above by the frontal, anteriorly by the well-developed lacrymal and to a short extent by the maxilla, and below by the jugal, which reaches as far anteriorly as the anterior lower corner of the orbit. In the sirenians the orbit is bordered by the lacrymal, and anteriorly as well as below by the jugal, which reaches almost as far anteriorly and above as the anterior upper corner of the orbit.

(6.) The antorbital foramina are situated just below the orbits, a character common to the sirenians and proboscideans in contrast to the hyracoids, in which they are situated a considerable distance anterior to the orbits.

(7.) A large fossa is present on either side, just below the orbit, a characteristic of the proboscideans in contrast to the hyracoids and sirenians.

(8.) The zygomatic arches are widest posteriorly, as in many sirenians and proboscideans. In the hyracoids the maximum width is at the middle of the arch.

(9.) As already stated under *C* (10) and *D* (5), the anterior, as well as posterior, limit of the jugal of this genus shows a marked proboscidean characteristic; the jugal differs from that of the hyracoids in its much



less anterior extension; and from that of the sirenians in its much less anterior and much more posterior extension.

(10.) As already stated under *C* (17), the condylar foramen is confluent with foramen lacerum posterius, a characteristic of the proboscideans in striking contrast to both the hyracoids and sirenians, except some individuals of modern *Manatus*.

(11.) The glenoid fossa and paroccipital process are close together, as in the proboscideans. In the hyracoids and sirenians they are widely separated.

(12.) The ascending bars of the mandible are very wide antero-posteriorly, being not very much narrowed upwards, so that the mandibular condyles are very far from the coronoid processes. This character is common to both the sirenians and proboscideans in contrast to the hyracoids.

(13.) The region of the mandibular angle projects very strongly downwards, so that the lower border of the ramus is concave just anterior to this region, as in *Palæomastodon* and the sirenians but in contrast to the hyracoids and other proboscideans.

(14.) The upper tusks correspond to the second incisors and are widely separated from each other, a characteristic of the proboscideans in contrast to the hyracoids and many sirenians. The first and second incisors are arranged almost interno-externally, instead of being antero-posteriorly, also a distinctive character from both the hyracoids and sirenians.

(15.) The cheek-teeth are very large in proportion to the size of the skull, a characteristic of the proboscideans in contrast to the hyracoids and especially sirenians.

(16.) The two rows of the upper cheek-teeth to the tusks are almost linear and parallel to each other, a characteristic of the proboscideans in contrast to the hyracoids and sirenians, though those of some individuals of the modern *Manatus* are rather linear and parallel within the limit of the cheek-teeth.

(17.) The premolars are very large and wide in proportion to the size of the molars, a peculiar characteristic of this genus in contrast to the hyracoids, earlier as well as certain later sirenians, and other proboscideans. The modern *Manatus*, however, has large premolars in proportion to the size of the molars.

Among these seventeen characters examined, nine, viz. (2), (5), (7), (9), (10), (11), (14), (15), and (16), are characteristics of the proboscideans in contrast to both the hyracoids and earlier or later sirenians; five,



*viz.*, (3), (6), (8), (12) and (13), are common to both the sirenians and proboscideans in contrast to the hyracoids; two, *viz.* (1) and (4), are common to this genus and the sirenians in contrast to both the hyracoids and other proboscideans; and one, *viz.* (17), is a peculiar characteristic of this genus as against all the hyracoids, sirenians, except modern *Manatus*, and other proboscideans. It may easily be recognized that *Mæriotherium* has many characteristics of the proboscideans, many characters common to both proboscideans and sirenians in contrast to the hyracoids, and quite a few characters common to this genus and the sirenians in contrast to both the hyracoids and other proboscideans.

#### *E.*—CHARACTERS IN COMMON WITH THE SIRENIANS

- (1.) Skull, as well as occiput, very low (*A* 1 and *C* 2).
- (2.) Mid-cranial region long, slender and tubular (*D* 1).
- (3.) External nares situated a distance behind anterior end of skull (*A* 3 and *D* 3).
- (4.) Orbits situated very anteriorly (*D* 4).
- (5.) Antorbital foramina situated just below orbits (*D* 6).
- (6.) Zygomatic arches widest posteriorly (*D* 8).
- (7.) The elevated external auditory openings (*A* 4 and *C* 13).
- (8.) The general shape and proportions of the frontal lobes, temporal lobes, and cerebellum, except the olfactory lobes, of the brain-case cast of *Mæriotherium* much resemble those of *Eosiren* (Andrews' figure<sup>1</sup>), but not so much those of *Eotherium* (Owen's figure<sup>2</sup> and Abel's figure<sup>3</sup>). This resemblance has been cited by Dr. Andrews and Prof. Gregory. It might to a great extent be due to convergence, owing chiefly to the similarity of their evolutionary stages, as may be judged from the facts that the olfactory lobes of *Mæriotherium* are quite different from those of the sirenians and that the brain-case cast of *Eotherium*, which is geologically older than both *Eosiren* and *Mæriotherium*, differs from that of *Mæriotherium* much more than does that of *Eosiren*.
- (9.) Ascending bars of the mandible incline slightly forwards (*C* 19).
- (10.) Ascending bars of the mandible very wide antero-posteriorly, being not very much narrowed upwards (*D* 12).
- (11.) The region of the mandibular angle projects very strongly downwards, so that the lower border of the ramus is concave just anterior to this region (*D* 13).

<sup>1</sup>1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt.,' Brit. Mus., p. 202, text-fig. 65.

<sup>2</sup>1875, Quart. Journ. Geol. Soc. London, XXXI, p. 100, Pl. III.

<sup>3</sup>1913, Palæontogr., LIX, Pl. (IV) XXXIII, figs. 3-5.



- (12.) Symphysis comparatively short (C 21).
- (13.) Full number of the upper incisors and canines present (C 24).
- (14.) Cheek-teeth bunodont showing an inclination to be lophodont (C 26).
- (15.) The scapula and humerus of *Mæritherium* resemble those of *Eosiren*. (Andrews.)
- (16.) The pelvis of *Mæritherium* more or less resembles that of *Eotherium*. (Andrews.)

Among these sixteen characters examined, five, *viz.* (3), (5), (6), (10), and (11), are common to both the proboscideans and sirenians in contrast to the hyracoids; four, *viz.* (1), (9), (12), and (13), are common to this genus, the sirenians, and hyracoids in contrast to the other proboscideans; three, *viz.* (8), (15), and (16), are common vaguely to this genus and the earlier sirenians; two, *viz.* (2) and (4), are common to this genus and the sirenians in contrast to the hyracoids and other proboscideans; one, *viz.* (7), is common to many groups of the ungulates. It may easily be recognized that the characters common to the proboscideans and sirenians but not found in the hyracoids are rather numerous, while there are but a few characters common to *Mæritherium* and the sirenians as against the hyracoids and other proboscideans.

F.—CHARACTERS DISTINCTIVE FROM THE SIRENIANS

- (1.) Skull very short in comparison with the zygomatic width (C 1).
- (2.) Sagittal crest well developed (C 3).
- (3.) Snout very short (C 4).
- (4.) Snout is wide (C 4 and D 2).
- (5.) The backwardly retired external nares face forwards, with their posterior border not rounded, as a characteristic of the proboscideans in contrast to the sirenians (B 3).
- (6.) Premaxilla and frontal separated from each other by the maxilla and nasal, which meet in the naso-maxillary suture (C 5).
- (7.) Orbits very small and shallow, as in the proboscideans. In the modern *Manatus* the orbits are likewise small but not shallow.
- (8.) In the lateral view the orbit is bordered above by the frontal, and forwards as well as below by the maxilla, the jugal reaching anteriorly only as far as the lower posterior corner of orbit (D 5).
- (9.) Roofs of the orbits not flared upwards, and the anterior borders of the same not projected outwards (A 2, B 2, and C 6).
- (10.) Antorbital foramina not extremely large or conspicuous (C 7).
- (11.) A large infraorbital fossa (D 7).



(12.) The outer borders of the snout and zygomatic arches in upper or lower view form together a very smooth, continuous curve on either side (*C 8*).

(13.) Zygomatic arches set very low and not very stout (*B 1* and *C 9*).

(14.) Jugals extend from posterior lower corners of the orbits to back of glenoid fossæ (*C 10* and *D 9*).

(15.) Zygomatic process of squamosal reaches anteriorly only to middle of zygomatic arch (*C 11*).

(16.) Upper limit of squamosal considerably below top of the parietal surface (*C 12*).

(17.) Auditory meatus fairly well closed inferiorly (*C 14*).

(18.) Squamosal, supraoccipital and exoccipital fully in contact, so that periotic is not exposed on occipital surface (*C 15*).

(19.) Pterygoid processes (pterygoid, alisphenoid and the posterior portion of palatine) not especially stout and do not project downwards to level of grinding surface of upper cheek-teeth (*C 16*).

(20.) Posterior alisphenoid canals and foramina ovalia distinct from the more posteriorly located foramina, and the condylar foramina are confluent with the more anteriorly located foramina (*C 17* and *D 10*).

(21.) Paroccipital processes thin antero-posteriorly (*C 18*).

(22.) Glenoid fossa and paroccipital process approximated (*D 11*).

(23.) Olfactory lobes of the brain-case cast very large (*B 4* and *E 8*).

(24.) Mandibular rami not conspicuously bent downward behind symphysis (*C 20*).

(25.) Symphysial depression is on upper, but not upper posterior or posterior surface of symphysis (*C 22*).

(26.) Anterior mental foramina are not conspicuously large (*C 23*).

(27.) The second, not the first, incisors of both jaws are enlarged and tusk-like (*C 25* and *D 14* in part).

(28.) First and second incisors of both jaws arranged not antero-posteriorly but interno-exteriorly (*D 14* in part).

(29.) Cheek-teeth very large in proportion to size of skull (*D 15*).

(30.) The two rows of the upper cheek-teeth to the tusks are almost linear and parallel (*D 16*).

(31.) Premolars large and wide in proportion to size of molars (*D 17*).

(32.) Scapula like that of sirenians in the posterior sweep of blade, but the very well developed coracoid process is an important distinction. (Andrews.)



(33.) Humerus resembling that of sirenians in certain characters, but differs notably in its length and slenderness, in the very well developed supinator ridge, in details of the shape of the distal end, etc. (Andrews.)

(34.) Pelvis resembling that of *Eotherium*, but differing in the more distinctly developed sacral surface, in position of the fossa for attachment of rectus femoris muscle and in the larger and less rounded obturator foramen. (Andrews.) As to *Eosiren*, which was contemporaneous with *Mæriotherium* and the later sirenians, their pelves are much more distinctly different.

Among these thirty-four characters examined, thirteen, *viz.* (2), (9), (10), (12), (13), (15), (16), (17), (18), (19), (21), (25), and (26), are common to both the hyracoids and proboscideans in contrast to the sirenians or earlier sirenians; ten, *viz.* (4), (8), (11), (14), (20), (22), (27), (28), (29), and (30), are characteristic of the proboscideans in contrast to both the hyracoids and earlier or later sirenians; three, *viz.* (5), (7) and (23), are characteristic of the proboscideans in contrast, at least, to the earlier or later sirenians; three, *viz.* (32), (33), and (34), are characters vaguely distinctive of this genus from the earlier or later sirenians; three, *viz.* (9), (13), and (23) [these characters are referred to in duplicate], are characters of some of the terrestrial mammals in contrast to the aquatic ungulates; and one, *viz.* (31), is characteristic of this genus in contrast to all the hyracoids, sirenians, and other proboscideans or earlier forms of these groups. It may easily be recognized that *Mæriotherium* has many characters common to both the hyracoids and proboscideans in contrast to the earlier or later sirenians, and many characteristics of the proboscideans in contrast to both the hyracoids and later sirenians or earlier sirenians.

#### G.—PROBOSCIDEAN CHARACTERS

(1.) Sagittal crest well developed, as in *Palæomastodon* (C 3 and F 2).

(2.) Snout wide (C 4, D 2, and F 4).

(3.) External nares retracted, though to a short extent, and facing forwards; their posterior borders are not rounded but indented by the insertion of the anterior ends of nasals (A 3, B 3, D 3, E 3, and F 5).

(4.) Orbits very small (F 7).

(5.) In lateral view the orbit is bordered above by the frontal, and forwards as well as below by the maxilla, the jugal reaching only as far anteriorly as the lower posterior corner of the orbit (D 5 and F 8).



(6.) Roofs of the orbits not flared upwards and the anterior borders of the same not projected outwards (*A* 3, *B* 2, *C* 6, and *F* 9).

(7.) Antorbital foramina situated just below orbits (*D* 6 and *E* 5).

(8.) Antorbital foramina not very large or conspicuous (*C* 7 and *F* 10).

(9.) A large fossa is present on either side, just below the orbit (*D* 7 and *F* 11).

(10.) Outer borders of the snout and zygomatic arches in upper or lower view form together a smooth, continuous curve on either side (*C* 8 and *F* 12).

(11.) Zygomatic arches rather weak and situated low (*B* 1, *C* 9, and *F* 13).

(12.) Zygomatic arches widest posteriorly (*D* 8 and *E* 6).

(13.) Jugals extending from the posterior lower corners of orbits to back of glenoid fossæ (*C* 10, *D* 9, and *F* 14).

(14.) Zygomatic process of each squamosal reaching only as far anteriorly as about the middle of the zygomatic arch behind the orbit (*C* 11 and *F* 15).

(15.) Upper limit of squamosal considerably below the level of the tops of the parietal surface (*C* 12 and *F* 16).

(16.) Auditory meatus fairly well closed in lower view (*C* 14 and *F* 17).

(17.) Squamosal, supraoccipital and exoccipital fully in contact all together, so that the periotic is not exposed on the occipital surface (*C* 15 and *F* 18).

(18.) Pterygoid processes, each of which consists of the pterygoid, alisphenoid and the posterior portion of palatine, not exceedingly stout and not projecting downwards so far as to reach the level of the grinding surface of the upper cheek-teeth (*C* 16 and *F* 19).

(19.) Posterior alisphenoid canals and foramina ovalia distinct from the more posteriorly located foramina; condylar foramina confluent with the more anteriorly located foramina (*C* 17, *D* 10, and *F* 20).

(20.) Paroccipital processes not very stout and thick, but thin antero-posteriorly (*C* 18 and *F* 21).

(21.) Glenoid fossa and paroccipital process on either side set close to each other (*D* 11 and *F* 22).

(22.) Olfactory lobes of the brain-case cast very large (*B* 4, *E* 8, and *F* 23).

(23.) Ascending bars of mandible very wide antero-posteriorly, being very narrow upwards (*D* 12 and *E* 10).



(24.) Region of the mandibular angle projecting very strongly downwards, so that the lower border of the ramus is concave just anterior to this region (*D* 13 and *E* 11).

(25.) Symphyseal depression on the upper, but not upper posterior or posterior surface of the symphysis (*C* 22 and *F* 25).

(26.) Anterior mental foramina not very large or conspicuous (*C* 23 and *F* 26).

(27.) Second incisors of both jaws enlarged and tusk-like (*C* 25, *D* 13, and *F* 27).

(28.) Upper tusks, which correspond to the second incisors, widely separated from each other (*D* 14).

(29.) Lower incisors very close set and forming together something like a spade as a whole (*B* 5).

(30.) Cheek-teeth bunodont showing an inclination to be lophodont (*C* 26 and *E* 14).

(31.) Cheek-teeth very large in proportion to size of skull (*D* 15 and *F* 29).

(32.) The two rows of the upper cheek-teeth are almost parallel to each other throughout (*D* 16 and *F* 30).

(33.) Vertebrae opisthocœlous instead of biplanous (*B* 6).

(34.) Lumbar vertebrae and sacrum well differentiated (*B* 7).

(35.) Anterior and posterior limbs well developed (*B* 8).

Among these thirty-five characters examined, seventeen, *viz.* (1), (6), (8), (10), (11), (14), (15), (16), (17), (18), (20), (25), (26), (29), (33), (34), and (35), are common to both the proboscideans and hyracoids in contrast to the recent or earlier sirenians; eleven, *viz.* (2), (3), (5), (9), (13), (19), (21), (27), (28), (31), and (32), are characteristic of the proboscideans in contrast to both the hyracoids and the earlier or later sirenians; seven, *viz.* (6), (11), (22), (29), (33), (34), and (35) [these characters are referred to in duplicate], are characters of some of the terrestrial mammals in contrast to the aquatic ungulates; four, *viz.* (7), (12), (23), and (24), are common to both the proboscideans and sirenians in contrast to the hyracoids; two, *viz.* (4) and (22), are characteristic, at least, of the proboscideans in contrast to the recent or earlier sirenians; and one, *viz.* (30), is common to all the proboscideans, sirenians and hyracoids. It may easily be recognized that *Mærittherium* has many characters common to both the proboscideans and hyracoids in contrast to the sirenians, and many characteristics of the proboscideans in contrast to both the hyracoids and sirenians.



## H.—PECULIAR AND PRE-PALÆOMASTODONT CHARACTERS

(1.) *Mæritherium* is very peculiar in having the skull very short in comparison with the zygomatic width. In the series of *Palæomastodon*, *Trilophodon*, and *Megabelodon*, the first is more short-skulled than the second, and the second is more so than the third. Now, *Mæritherium* is more short-skulled than *Palæomastodon*.

(2.) *Mæritherium* is very peculiar in having the naso-fronto-parietal region very long in proportion to the length of the snout. This region is slightly longer than the premaxillary region in *Palæomastodon*; nearly as long as, or slightly shorter than, the latter in *Trilophodon*; and much shorter in *Megabelodon*. In *Mæritherium* the naso-fronto-parietal region is exceedingly long, being very much longer than the premaxillary region.

(3.) *Mæritherium* is very peculiar in having the zygomatic arches very long in proportion to the length of the skull. The zygomatic arches in the region behind the orbits are, in *Mæritherium*, about as long as, or slightly longer than, three-fifths the basilar length; in *Palæomastodon* and *Trilophodon*, one-half to two-fifths; and in *Megabelodon*, two-fifths to one-third.

(4.) *Mæritherium* is very peculiar in having the almost tubular mid-cranial region, the interorbital width being exceedingly small. This width is about one-half the zygomatic width in *Palæomastodon*; about two-thirds in *Trilophodon*; and about three-fourths in *Megabelodon*. Now, in *Mæritherium*, this width is about one-third the zygomatic width.

(5.) The sagittal crest is very well developed in *Mæritherium*, occupying about one-half, or more, of the distance between the anterior ends of the nasals and the top of the lambdoid crest. The sagittal crest is present also in *Palæomastodon*, occupying less than one-third the same distance. In *Trilophodon* and *Megabelodon*, this crest is no longer present, but is replaced by a pair of temporal crests; the intertemporal width is very small in the former, and rather great in the latter.

(6.) The very anterior situation of the external nares of *Mæritherium* is also very peculiar among the proboscideans. The external nares are situated just above the diastema between C and P<sup>2</sup> in *Mæritherium*; almost above P<sup>4</sup> or M<sup>1</sup> in *Palæomastodon*; almost above M<sup>2</sup> in *Trilophodon*; and almost above M<sup>3</sup> in *Megabelodon*.

(7.) The very anterior situation of the orbits of *Mæritherium* is also very peculiar. The orbits are situated just above P<sup>2-3</sup> in *Mæritherium*; just above M<sup>1-2</sup> in *Palæomastodon*; just above M<sup>2-3</sup> in *Trilophodon*; and just above M<sup>3</sup> in *Megabelodon*.



(8.) The relative position of the external nares and orbits of *Mæri-therium* is also very peculiar among the proboscideans. In *Palæomastodon*, the posterior border of the external nares lies just a little before the anterior borders of the orbits; in *Trilophodon* the former lies a little or moderately behind the latter; and in *Megabelodon* the former lies far behind the latter. Now, in *Mæri-therium* the former lies moderately before the latter.

(9.) The external auditory openings are situated above the level of the upper borders of the occipital condyles in *Mæri-therium*; about at the same level in *Palæomastodon*; about at the same level as the level of the middle of the occipital condyles in *Trilophodon*; and about at the level of the lower borders of the occipital condyles in *Megabelodon*. Moreover, it should be remembered that many short-jawed mastodonts and elephants have the external auditory openings situated above the level of the upper borders of the occipital condyles. As already stated under A (4) it appears that those proboscideans which have short skulls and erect to anteriorly inclined ascending bars of the mandibles, have highly situated external auditory openings, and those proboscideans which have long skulls and posteriorly inclined ascending bars of the mandibles, have lowly situated auditory openings.

(10.) The anterior limits of the temporal vacuities, in palatal view, of *Mæri-therium* lie almost on the frontal plane, which passes through the boundaries between  $P^4$  and  $M^1$ . Those of *Palæomastodon* lie almost on the frontal plane, which passes through somewhere between the first ridge of  $M^2$  and that of  $M^3$ ; and those of *Trilophodon* and *Megabelodon* lie on the frontal plane which cuts some parts of  $M^3$ .

(11.) The mandible of *Mæri-therium* is short and is about as long as or slightly shorter than the skull. That of *Palæomastodon* is slightly longer than the skull; that of *Trilophodon* much longer; and that of *Megabelodon* nearly twice as long.

(12.) The anterior part, free of cheek-teeth, of the mandible of *Mæri-therium* is peculiarly short, being only about as long as one-sixth the mandible. That of *Palæomastodon* is about two-fifths as long as the mandible; that of *Trilophodon* three-sevenths to one-half as long; and that of *Megabelodon* one-half to three-fifths as long.

(13.) The ascending bars of the mandible of *Mæri-therium* incline slightly forwards. Those of *Palæomastodon* are nearly erect or incline slightly backwards; and those of *Trilophodon* and *Megabelodon* incline more distinctly backwards.

(14.) The region of the mandibular angle of *Mæri-therium* projects markedly downwards, so that there is a distinct concavity on the lower



border of the mandibular ramus, just anterior to this region. The mandible of *Palæomastodon* has, also, such a convexity and a concavity on each mandibular ramus; but these characters in this genus are more feeble and less marked than in *Mæriotherium*. *Trilophodon* has either such a convexity and a concavity, very feeble, or none at all, and *Megabelodon* none at all.

(15.) The lower border of the mandible of *Mæriotherium* bends upwards at about the part corresponding to the posterior end of the symphysis. That of *Palæomastodon* is almost linear or very slightly bends downwards at about the same part; and that of *Trilophodon* and *Megabelodon* more distinctly bends downwards.

(16.) The symphysis of the mandible of *Mæriotherium* is rather short. That of *Palæomastodon* is fairly long; that of *Trilophodon* very long; and that of *Megabelodon* extremely long.

(17.) The symphysial depression of *Mæriotherium* lies among  $I_2$  and  $P_{2-3}$ , occupying nearly the entire length of the symphysial groove; that of *Palæomastodon* lies a distance anterior to the posterior border of the symphysial region as well as to the premolars, occupying an anterior part of symphysial groove; that of *Trilophodon* lies farther anterior than the posterior border of symphysial region as well as the cheek-teeth, occupying only an anterior part of the symphysial groove; and that of *Megabelodon* lies still farther anterior to the same, occupying still less part of symphysial groove.

(18.) The dental formulæ of *Mæriotherium*, *Palæomastodon*, *Trilophodon* and its allied Mastodonts, are:

|                            |                             |                       |                                         |                     |
|----------------------------|-----------------------------|-----------------------|-----------------------------------------|---------------------|
| <i>Mæriotherium</i> :      | $I_{(1).1.(1)}^{(1).1.(1)}$ | $C_{(1).1.(1)}^{(1)}$ | $P_{0.1.1.1}^{0.1.1.1}$                 | $M_{1.1.1}^{1.1.1}$ |
| <i>Palæomastodon</i> :     | $I_{0.1.0}^{0.1.0}$         | $C_0^0$               | $P_{0.0.1.1}^{0.1.1.1}$                 | $M_{1.1.1}^{1.1.1}$ |
| <i>Trilophodon</i> , etc.: | $I_{0.1.0}^{0.1.0}$         | $C_0^0$               | $P_{0.0-(1).(1).(1)}^{0.0-(1).(1).(1)}$ | $M_{1.1.1}^{1.1.1}$ |

(19.) The upper tusks of *Mæriotherium* are very short in comparison with those of the other proboscideans. Those of *Palæomastodon* are moderately long; those of *Trilophodon* are very long, being distinctly longer than those of the preceding; those of *Megabelodon* are also very long, being longer in the adult than those of the preceding; and those of the short-jawed mastodonts and elephants, with almost horizontal to upwardly bent upper tusks, are excessively long, being much longer in the adult than those of *Trilophodon* and *Megabelodon*.

(20.) *Mæriotherium* is peculiar in having the premolars very large in proportion to the size of the molars or, in other words, in having the series of the cheek-teeth increase their size backwards very gradually. The



degree of increase in size backwards of the series of the cheek-teeth is more rapid in *Palæomastodon* than in *Mæriotherium*; more so in *Trilophodon* than in *Palæomastodon*; and more so in *Megabelodon* than in *Trilophodon*.

(21.) The ridge formulæ of the cheek-teeth of *Mæriotherium*, *Palæomastodon*, and *Trilophodon*, are as follows:

|                                         |                                     |                                                    |                                                        |
|-----------------------------------------|-------------------------------------|----------------------------------------------------|--------------------------------------------------------|
| <i>Mæriotherium</i> :                   | $\text{Dm} \frac{???}{??2}$         | $\text{P} \frac{1.1(+1).1(+1)}{1(+1).1(+1).1(+1)}$ | $\text{M} \frac{2.2.2.(+1)}{2.2.2.(+1)}$               |
| <i>Palæomastodon</i> (A):               | $\text{Dm} \frac{???}{???}$         | $\text{P} \frac{1. \quad 1. \quad 2.}{1.1(+1).2}$  | $\text{M} \frac{2(+1).2(+1).2(+1)}{2(+1).2(+1).2(+1)}$ |
| <i>Palæomastodon</i> (B) <sup>1</sup> : | $\text{Dm} \frac{1.2.3}{1.2.3}$     | $\text{P} \frac{1. \quad 1-1(+1).2}{1(+1).2}$      | $\text{M} \frac{3.3.2(+1)-3}{3.3.3-3(+1)}$             |
| <i>Trilophodon</i> :                    | $\text{Dm} \frac{1-2.2.3}{1-2.2.3}$ | $\text{P} \frac{2.2}{2.2}$                         | $\text{M} \frac{3.3.4}{3.3.4}$                         |

(22.) In *Mæriotherium* all the three pairs of premolars and the three pairs of molars of both jaws were functional at the same time. In *Palæomastodon* all the three pairs of premolars and three pairs of molars of the upper jaw and the two pairs of premolars and three pairs of molars of the lower jaw were so; in *Trilophodon* only three or two pairs of cheek-teeth of both jaws were so; and in *Megabelodon* only two pairs of cheek-teeth of both jaws were so.

(23.) In *Mæriotherium* the trefoil pattern of cusps of the cheek-teeth is not developed at all. In one group of *Palæomastodon* also, such a pattern of cusps is not developed, while in another group of the same genus such a pattern of cusps is more or less well developed. In *Trilophodon*, *Megabelodon*, *Chærolophodon*, *Rhynchotherium*, *Dibelodon*, *Tetralophodon*, and *Pentalophodon*, such a trefoil pattern of cusps is very well developed. Thus *Mæriotherium* stands before *Palæomastodon* in this character also. Again, in *Zygalophodon* and *Mastodon* such a pattern of cusps is not developed at all. Thus, *Mæriotherium* appears to represent a generalized type of both the *Palæomastodon* (B)—*Trilophodon*—*Megabelodon* phylum and the *Palæomastodon* (A)—*Zygalophodon*—*Mastodon* phylum, within the limits of the above-mentioned character.

In all the twenty-three characters examined, *Mæriotherium* is structurally a pre-*Palæomastodont* type, so far as we admit the conception that *Palæomastodon*, *Trilophodon*, and *Megabelodon* form together a fair series of evolutionary stages. It is, of course, beyond doubt that the structural gap between *Mæriotherium* and *Palæomastodon* is fairly great. Notwithstanding such a great structural gap between them, yet the fact should not be neglected that *Mæriotherium* stands structurally before *Palæomastodon* in so many characters as just stated above.

<sup>1</sup>I am going to distinguish this group as a genus distinct from the typical *Palæomastodon*. See my future paper now being prepared.



I have adopted chiefly the series of *Palæomastodon*, *Trilophodon*, and *Megabelodon* to judge the structural position of *Mæritherium*, simply because these three genera appear, as declared by Professor Osborn, to represent structurally, geologically, and palæozoögeographically a fair series, which might have evolved in one and the same direction (not one and the same evolutionary course). As to the short-jawed mastodonts and elephants, they had their evolutionary directions obviously different from that of the just-mentioned series.

#### I.—NATURAL POSITION OF MÆRITHERIUM

It may be evident from the preceding statements that *Mæritherium* differs strongly from either the hyracoids or the sirenians in many characters, on the one hand, and has many proboscidean and pre-Palæomastodont characters on the other hand. If much weight should be given to the sirenian resemblances of *Mæritherium*, then more weight should be given to its hyracoid resemblances. In my opinion *Mæritherium* is to be treated as a very archetypal member of the proboscideans as correctly stated by Andrews at the first.

*Mæritherium* has many pre-Palæomastodont characters. Consequently a presumed ancestral type of *Palæomastodon* should resemble *Mæritherium* in many characters. On the other hand, the structural gap between *Mæritherium* and *Palæomastodon* is fairly great. Then it might have happened, either that *Palæomastodon* arose from a very much earlier stage of *Mæritherium*, or from an ancestral type, yet unknown to us, which resembled *Mæritherium* in certain ways. At any rate, *Mæritherium* appears to me to stand near the phylogenetic base of the *Palæomastodon* phylum, if not actually ancestral to the same.

We are familiar with the conceptions that the short-jawed type of *Tetralophodon* was not strictly an evolutionary successor to the last stage of *Trilophodon*; that *Stegodon* was not strictly an evolutionary successor to the last stage of *Tetralophodon* or *Pentalophodon*; and that *Elephas* was not an evolutionary successor to the last stage of *Stegodon*. We should not be surprised to see the evidences that *Palæomastodon* was not strictly an evolutionary successor to the last stage of *Mæritherium*.

#### J.—EVOLUTIONARY TENDENCIES IN THE EARLIER PROBOSCIDEANS

As already stated, the lower jaws of *Mæritherium*, *Palæomastodon*, *Trilophodon*, and *Megabelodon*, having their incisors formed together something like a spade, display a structure adapted to the digging and rooting in a terrestrial life. The mode of using such a lower jaw may sug-



gestively be conceived in observing the life-mode of the suids. In *Mæritherium*, however, the second pair of the lower incisors shows a tendency of being tusk-like, not as in the suids. This proper tendency observed in *Mæritherium* may be of very great significance.

As I have already stated in my study of the palæobiology of *Desmostylus*,<sup>1</sup> the development of the tusks and jaws appears to me to correlate with each other in two ways: first, the antero-posterior elongation of the tusks correlates with that of their own jaw; and, second, the antero-posterior elongation of the tusks plus jaw correlates with that of the opposite tusks plus jaw, so far as the tusks of both jaws are functionally mating. The tendency of the lower, as well as the upper, second incisors to be tusk-like, observed in *Mæritherium*, is very interesting from this point of view.

The external nares of *Mæritherium* show a tendency to retire backwards. This character may also be very important for the problem of the phylogeny of the proboscideans, because such a retirement of the external nares correlates with the development of a retractile or prehensile upper lip or a proboscis, so far as the retired external nares faces forwards and its posterior border is indented by the insertion of the anterior ends of the nasals. Doubtless *Mæritherium* might not have a well-formed proboscis, though, again doubtless, it might have a more or less retractile or prehensile upper lip—a first step toward a proboscis. Judging from the degree of the retirement of the external nares, the presumed prehensile upper lip of *Mæritherium* might be in a condition more rudimentary than that of modern tapirs.

The retirement of the external nares might yield a suitable space for the development of the upper incisor tusks, for well-developed and heavy upper tusks need long and powerful premaxillæ for the support of their bases. If the case be the canine tusks, there may be no need for either the external nares to retire or for the premaxillæ to become long and powerful; the upper canine tusks have their support in the maxillæ and are situated lateral to the external nares. Such a condition is clearly seen in the upper canine tusks of *Desmostylus*. The condition seen in *Mæritherium*, on the contrary, is quite similar to that observed in *Eosiren*, *Halitherium*, *Halicore*, etc., as well as *Palæomastodon*, mastodons, and elephants.

So far as the characters are concerned, we can fairly conceive an evolutionary stage somewhat resembling *Palæomastodon* by supposing a further development of the evolutionary tendencies already acquired by

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<sup>1</sup>1918, Sci. Rep. Tôhoku Imp. Univ., Series B, III, No. 2.



*Mæriotherium*. But, if we neglect *Mæriotherium*, we may not be able to conceive at all how the structures observed in the *Palæomastodon* phylum have arisen.

K.—PHYLOGENETIC RELATIONS AMONG THE HYRACOIDS, EARLIER PROBOSCIDEANS, AND SIRENIANS

That the proboscideans and sirenians are very closely related to each other in their earlier stages of evolution has been maintained by many eminent authors, such as Blainville, Andrews, Osborn, Gregory, etc. It is, of course, very obvious that their earlier stages resemble each other in certain ways. Nevertheless, it is also obvious that the differences observed between the series of *Prorastomus*, *Eotherium*, *Prosiren*, *Eosiren*, *Miosiren*, *Halitherium*, etc., and the series of *Mæriotherium*, *Palæomastodon*, *Trilophodon*, and *Megabelodon* are very great. The first series started from long-skulled types (*Prorastomus*, *Eotherium*, etc.) and became more and more short-skulled, while the second series started from short-skulled types (*Mæriotherium* and *Palæomastodon*) and became more and more long-skulled (though the naso-fronto-parietal region became progressively shortened). So far as the length of the skull is concerned, the two series took their evolutionary courses, not parallel nor divergent, but they crossed each other. Then, the divide or common base of these two series might naturally be traced back very far from the stage of *Mæriotherium*. Consequently, the phylogenetic relation between the two series should be somewhat less close than considered by those authors who emphasize chiefly the resemblances between *Mæriotherium* and the earlier sirenians.

A number of the similarities between *Mæriotherium* and the earlier sirenians should be due to their phylogenetic closeness; another series of resemblances should be due to convergence, owing to the fact that *Mæriotherium* is situated somewhat near the cross-way of the evolutionary courses of the two series; and still other similarities should be due to their being primitive, being common to all the three groups of the hyracoids, earlier sirenians, and earliest proboscideans. Doubtless no known sirenian can be looked upon as an ancestral type of *Mæriotherium* and doubtless *Mæriotherium* cannot be looked upon as an ancestral type of any known sirenian.

*Mæriotherium* resembles the hyracoids in many characters already stated; and the resemblance between them appears to be rather stronger than even that between *Mæriotherium* and the sirenians. On the other hand, *Mæriotherium* differs from the hyracoids also in many characters



already stated. Doubtless no known hyracoid can be looked upon as an ancestral type of *Mæriotherium*.

Consequently, both the sirenians and proboscideans might have descended from unknown ancestors which stand even before the hyracoids so far as known.

#### SYSTEMATIC

Andrews distinguished three species of *Mæriotherium*, viz., *M. lyonsi*, a larger form of both the Qasr-el-Sagha and Fluvio-marine Formations; *M. gracile*, a smaller form of the Qasr-el-Sagha Formation; and *M. trigodon* a smaller form of the Fluvio-marine Formation. Schlosser divided Andrews' *M. lyonsi*, from the stratigraphical and morphological standpoint, into two species, viz., *M. lyonsi*, restr., a larger form of the Qasr-el-Sagha Formation, and *M. andrewsi*, a larger form of the Fluvio-marine Formation. Further, he inclined to look upon the larger and smaller forms of each formation as a sexual difference within one and the same species; consequently, he recognized only two species of *Mæriotherium*, viz., *M. lyonsi*, including both the larger and smaller forms of the Qasr-el-Sagha Formation and *M. andrewsi*, including both the larger and smaller forms of the Fluvio-marine Formation. If his view be at all correct, his *M. andrewsi* should be called *M. trigodon*, according to the law of priority.

As far as judged from the material belonging to the American Museum, which includes two skulls corresponding to the larger and smaller forms of the Fluvio-marine Formation, the two forms cannot at any rate be looked upon as a sexual difference of one and the same species; the smaller skull has much stronger sagittal and occipital crests and a much wider occiput, and the external auditory openings are much more distant from each other, than in the larger skull. This fact may indicate the specific distinction of the larger and smaller forms. Moreover, I noticed from the material of the American Museum and from Andrews' statement that the difference between the larger and smaller forms of the Qasr-el-Sagha Formation is greater than that between the larger and smaller forms of the Fluvio-marine Formation. Consequently, the two forms of the Qasr-el-Sagha Formation, also, might better be looked upon as two distinct species. Thus, I have come to recognize four species of *Mæriotherium*, which may be distinguished as follows:

(1.) Larger form of the Qasr-el-Sagha Formation. Lower premolars very short:  $P^{2-4}$ , ca. 69 mm. (Andrews); lower molars very long,  $M_{1-3}$ , ca. 104 mm. (Andrews). All the lower cheek-teeth very wide.  $P_2$ , triangular, its widest part corresponding to the posterior lobe.  $P^{2-4}$ , 67-78 mm.;  $M^{1-3}$ , 85 mm. (Andrews).....*M. lyonsi*.



(2.) Smaller form of the Qasr-el-Sagha Formation. Lower premolars not very short in comparison with the length of lower molars:  $P_{2-4}$ , ca. 62 mm. (specimens in the American Museum); lower molars very short:  $M_{1-3}$ , 83 mm. (specimen in the American Museum). All the lower cheek-teeth are narrow.  $P^{2-4}$ , 62 mm. (Andrews);  $M^{1-3}$ , 75—ca. 79 mm. (Andrews).....*M. gracile*.

(3.) Larger form of the Fluvio-marine Formation. Lower premolars not very short in comparison with the length of lower molars;  $P_{2-4}$ , 70 (specimen in the American Museum)—73 mm. (Andrews); lower molars rather long:  $M_{1-3}$ , 99 (Andrews)—100 mm. (specimen in the American Museum). All the lower cheek-teeth are narrow.  $P_2$ , fusiform in upper view, its widest part corresponding to the middle part.  $P^{2-4}$ , 70–75 mm. (Andrews);  $M^{1-3}$ , yet unknown, but  $M^{1-2}$ , ca. 61 mm. (British Museum cast in the American Museum). Skull large and heavily built. Sagittal crest rather weak. Zygomatic width rather small in comparison with the length of skull. Distance between the two external auditory openings, as well as the width of occiput, small, being smaller even than in the next form.....*M. andrewsi*.

(4.) Smaller form of the Fluvio-marine Formation. Lower premolars not very short in comparison with the length of lower molars:  $P_{2-4}$ , ca. 63 (specimen in the American Museum)—70 mm. (ditto, as well as Andrews); lower molars rather short:  $M_{1-3}$ , 93 (specimens in the American Museum)—98 mm. (Andrews). All the lower cheek-teeth very narrow:  $P_2$ , fusiform in upper view, its widest part corresponding to the middle part.  $P^{2-4}$ , 60–63 mm. (specimen in the American Museum);  $M^{1-3}$ , 83–85 mm. (ditto). Skull, small and lightly built. Sagittal and occipital crests very strong. Zygomatic width very large in comparison with the length of skull. Distance between the external auditory openings, as well as the width of occiput, very large.....*M. trigodon*.

### (1.) *Mæritherium lyonsi* Andrews

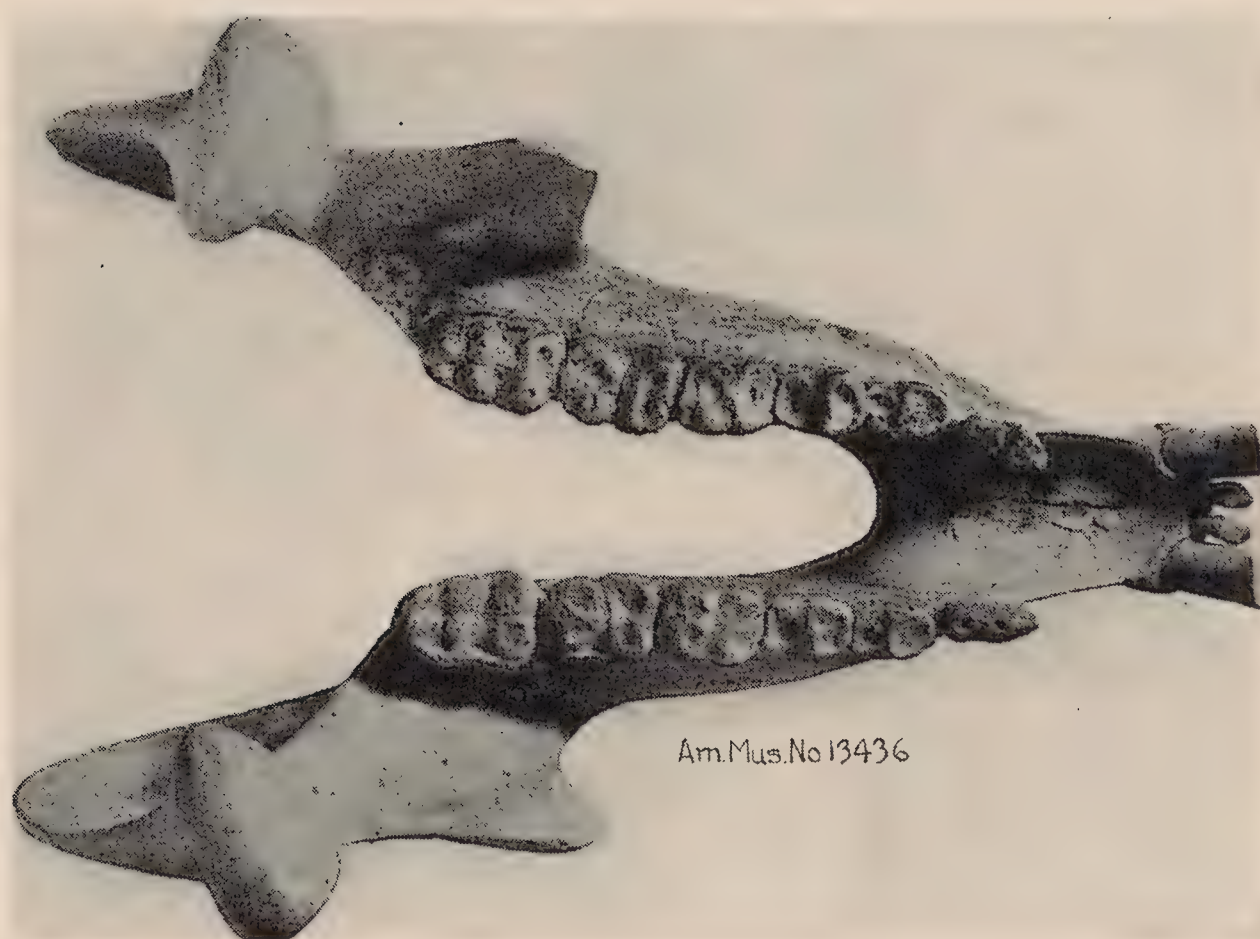
*M. lyonsi* ANDREWS, 1901, Tagebl. d. V. International Zool. Congr. Berlin, No. 6, p. 4<sup>1</sup>; ANDREWS, 1901, Geol. Mag., Decade IV, VIII, pp. 403–406, text-fig. 2; ANDREWS, 1903, Phil. Trans., Ser. B., CXCVI, pp. 113–117, text-figs. 14–17; ANDREWS, 1904, Geol. Mag., Decade V, I, pp. 109–112, text-fig. 1; ANDREWS, 1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt,' Brit. Mus., pp. 120–126, *pars*, Pl. x, figs. 1–5, Pl. XI, figs. 1–9. SCHLOSSER, 1911, 'Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients,' XXIV, pp. 131–135, Pl. XVI (VIII), figs. 1–5.

SPECIMENS.—No. 13444; two of the three fragments of mandibular rami of this specimen number appear to belong to this species. They are very peculiarly weathered, as a characteristic of the weathered specimens from the Qasr-el-Sagha Formation, with much-weathered and badly preserved molars *in situ*. Qasr-el-Sagha Formation of the Fayûm.

The dimensions of the teeth of these fragments, in comparison with those of Andrews' specimens, are tabulated as follows (in mm.):

<sup>1</sup>This paper was not seen by me.





1



2

Fig. 1. *Mæritherium lyonsi* Andrews. Mandible, Amer. Mus. No. 13436.  
One-fourth natural size. Superior view.

Fig. 2. *Mæritherium lyonsi* Andrews. Second upper right incisor tooth, Amer. Mus. No. 13434.

One-half natural size. Upper figure, internal view; lower figure, external view.



|                |   |        | Lower Teeth               |    |       | Upper Teeth |    |    |       |
|----------------|---|--------|---------------------------|----|-------|-------------|----|----|-------|
|                |   |        | No. 13444 ditto (Andrews) |    |       | (Andrews)   |    |    |       |
| P2             | { | length | ..                        | .. | 22    | 27          | .. | .. | ..... |
|                |   | width  | ..                        | .. | 16    | 23?         | .. | .. | ..... |
| P3             | { | length | ..                        | .. | 23    | 26.5        | .. | .. | ..... |
|                |   | width  | ..                        | .. | 21    | 29.5        | .. | .. | ..... |
| P4             | { | length | ..                        | .. | 25    | 23          | .. | .. | ..... |
|                |   | width  | ..                        | .. | 23    | 27.5        | .. | .. | ..... |
| M1             | { | length | ..                        | .. | 26.5  | 29          | .. | .. | ..... |
|                |   | width  | ..                        | .. | 24.5  | 27          | .. | .. | ..... |
| M2             | { | length | 29                        | 28 | 35    | 26?         | 30 | .. | ..... |
|                |   | width  | 25                        | 25 | 39    | 23.5        | 28 | .. | ..... |
| M3             | { | length | 40                        | 39 | 42    | ....        | 32 | .. | 37±1  |
|                |   | width  | 28                        | 28 | 30    | ....        | 28 | .. | 30±1  |
| Length of P2-4 |   |        | ..                        | .. | 69±1  | 68          | .. | 67 | ..... |
| Length of M1-3 |   |        | ..                        | .. | 104±1 | ....        | .. | 85 | ..... |



Fig. 3. *Mæritherium lyonsi* Andrews. Amer. Mus. No. 13444, left ramus of mandible, incomplete.  
One-half natural size. Superior view.

Andrews reported a skull with the two upper tusks, viz., I<sup>2</sup> which measure about 28 mm. in transverse as well as to and fro diameter, from the Qasr-el-Sagha Formation. This specimen might probably belong to the present species, as stated by Andrews.

(2.) *Mæritherium gracile* Andrews

*M. gracile*.—ANDREWS, 1902, Geol. Mag., Decade 4, IX, p. 292; ANDREWS, 1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt,' Brit. Mus., pp. 127-128, Pl. xvii, figs. 1-3; SCHLOSSER, 1911, 'Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients,' XXIV, pp. 131-132.

<sup>1</sup>These dimensions are estimated from Andrews' figures.



SPECIMENS.—No. 13443; mandible, with P<sub>3</sub>–M<sub>3</sub> of the left side and M<sub>1-3</sub> of the right side *in situ*. No. 13444; one of the three fragments of mandibular rami of this specimen number, with badly preserved molars *in situ*. No. 13445; fragment of a right mandibular ramus of a young individual, with the teeth broken away. No. 13446; fragment of a left mandibular ramus, with the crowns of the teeth broken away. All from the Qasr-el-Sagha Formation of the Fayûm.

The mandible of No. 13443 measures 305 mm. in length without incisors, 8.5 mm. in length of symphysis, 55 mm. and 50 mm. in the distance between the two first molars and the two last molars respectively, 225 mm. in the bicondylar width and 76 mm. in the height of the mandibular ramus at M<sub>1</sub> without the teeth. In this specimen the symphyisial depression already cited is observed to be present. In the fragmentary mandible of No. 13446, the same depression is clearly observed, also.

The dimensions of the cheek-teeth of the specimens at hand, in comparison with those of Andrews', are tabulated as follows (in mm.):

|                |        | Lower Teeth             |        |           | Upper Teeth |      |
|----------------|--------|-------------------------|--------|-----------|-------------|------|
|                |        | No. 13443<br>right-left |        | No. 13444 | (Andrews)   |      |
| P2             | length | ....                    | ....   | ..        | 22          | ..   |
|                | width  | ....                    | ....   | ..        | 18          | ..   |
| P3             | length | ....                    | 22     | ..        | 20          | ..   |
|                | width  | ....                    | 15     | ..        | 23          | ..   |
| P4             | length | ....                    | 21     | ..        | 20          | ..   |
|                | width  | ....                    | 18     | ..        | 21?         | ..   |
| M1             | length | 23                      | 23     | 22        | 23          | 25   |
|                | width  | 20                      | 19     | 19?       | 23          | 21   |
| M2             | length | 28                      | 28     | 27        | 24          | 27   |
|                | width  | 22.5                    | 23     | 22        | 25          | 23   |
| M3             | length | 34                      | 33     | ..        | 28          | 28   |
|                | width  | 24                      | 24     | ..        | 24          | 25   |
| Length of P2-4 |        | 63±                     | 63±    | ..        | 62          | ..   |
|                |        | (alveoli)               | ditto) |           |             |      |
| Length of M1-3 |        | 84                      | 84     | ..        | 75          | 79±1 |

The alveoli of each I<sub>1</sub> and I<sup>2</sup> of the mandible of No. 13443 measure 10 mm. and 20 mm. in transverse diameter, respectively; the lateral extension of, and the minimum distance between, the two alveoli of lower tusks are 50 mm. and 9 mm. respectively. The two alveoli of first

<sup>1</sup>This dimension is estimated from Andrews' figure.





Am. Mus. No. 13443

Fig. 4. *Mæritherium gracile* Andrews. Amer. Mus. No. 13443, left ramus of mandible, incomplete.

One-fourth natural size. Lateral view, left side.

incisors are situated just below and anterior to the part corresponding to minimum distance between the two alveoli of tusks. Judging from these alveoli, the lower first incisors might be located not strictly inside, but inside and below and anterior to, the pair of lower tusks, which might be rather closely set to each other. These lower tusks appear to be distinctly smaller than those of *M. lyonsi* and *andrewsi*.

### (3.) *Mæritherium andrewsi* Schlosser

*M. lyonsi* ANDREWS, 1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt,' Brit. Mus., pp. 128-129, *pars*, Pl. VIII, fig. 1, Pl. IX, figs. 1, 2, and 4.

*M. andrewsi* SCHLOSSER, 1911, 'Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients,' XXIV, pp. 130-131, *pars*.

SPECIMENS.—No. 13432; right half of a full-grown skull, without teeth, well preserved in the limit of the parts represented. No. 13434; right upper tusk, *viz.* I<sup>2</sup>, with well-worn crown. Extra no.; left first upper incisor, with imperfectly preserved crown. No. 13437, greater part of a mandible, with the right series of cheek-teeth, except P<sub>4</sub> which might have been accidentally lost in the life of the animal, and with left M<sub>2-3</sub> *in situ*. All from the Fluvio-marine Formation of the Fayûm.

As to the specific name, if Schlosser's own material, which he purposely described in his paper, be the type of his new species, then the specific name *andrewsi* cannot be adopted for the present species;



because his principal material, not the auxiliary specimen described by him, appears to be referred to *M. trigodon*. But, so far as judged from his statement, he appears to have founded his new species upon certain of Andrews' specimens and referred his own material to it with some doubt. Consequently, his specific name is to be preserved.

The skull of No. 13432 measures about 345 mm. in the length from the anterior end of nasal to the occipital crest (including a restored part to a short extent), about 380 mm. in the length from the anterior end of premaxilla to the outer posterior border of squamosal, about 300 mm. in the length from the anterior border of orbit to the outer posterior border of squamosal, about  $2 \times 45 = 90$  mm. in the distance between the postorbital processes of frontals, about  $2 \times 35 = 70$  mm. in the minimum width of the mid-cranial region, about  $2 \times 145 = 290$  mm. in the zygomatic width, about  $2 \times 78 = 156$  mm. in the distance between the upper borders of external auditory openings (including a restored part to a short extent), about  $2 \times 93 = 186$  mm. in the width of occiput (including a restored part to a short extent), and about 50 mm. in the length of the diastema between the alveoli of C and P<sup>2</sup>. In this skull the sagittal crest is developed, but much weaker than that of the skull of No. 13430, which is referred to *M. trigodon*, notwithstanding the former is much larger than the latter. The orbital region is fairly well preserved in this skull; the maxilla runs up along the anterior border of the orbit and meets both the nasal and frontal, and no undoubted lacrymal is observed, quite as stated by Andrews. If the lacrymal might originally be present at all, it might be located deep within the orbit: the bottom of the orbit of this skull is broken away.

The mandible of No. 13437 measures 310 mm. in length back from the anterior border of P<sub>2</sub>, 72 mm. and 75 mm. in height of ramus at P<sub>3</sub> and M<sub>1</sub> respectively without the teeth, and 205 mm. in height at condyle. The dimensions of the cheek-teeth of this specimen, in comparison with those of Andrews, are tabulated (in mm.) on p. 132.

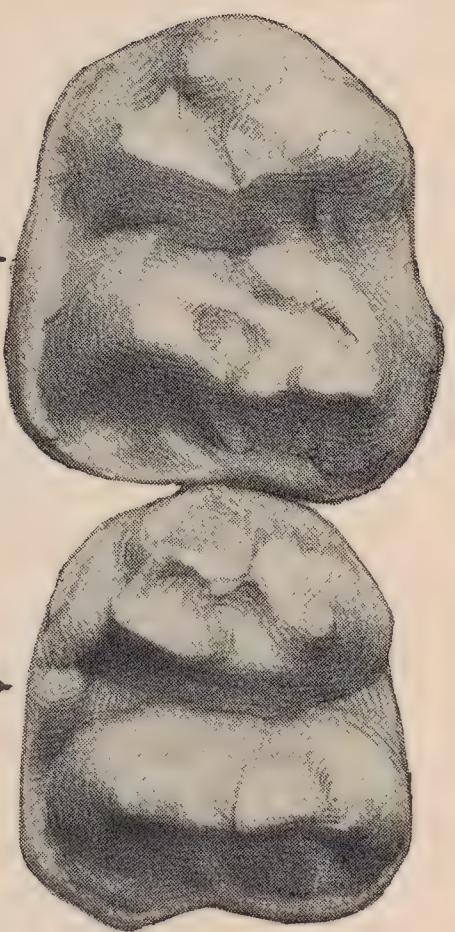
The first upper incisor of the extra-number at hand measures 16.5 mm. in the side to side, and 14.5 mm. in the to and fro, diameter of the

Fig. 5. Life-size comparison of molars of *Mærittherium* and *Palæomastodon* drawn for the Proboscidea Memoir by Mrs. L. M. Sterling under the direction of Henry Fairfield Osborn. A, Amer. Mus. No. 15898, *M. andrewsi* Schlosser (cast), upper molar teeth; B, Amer. Mus. No. 13431, *M. trigodon* Andrews, upper premolars and molars; C, Amer. Mus. No. 13437, *M. andrewsi* Schlosser, lower molars; D, Amer. Mus. No. 13449, *Palæomastodon* sp., upper molar; E, Amer. Mus. No. 14547, *Palæomastodon* species, lower molar. All but the last of the right side.



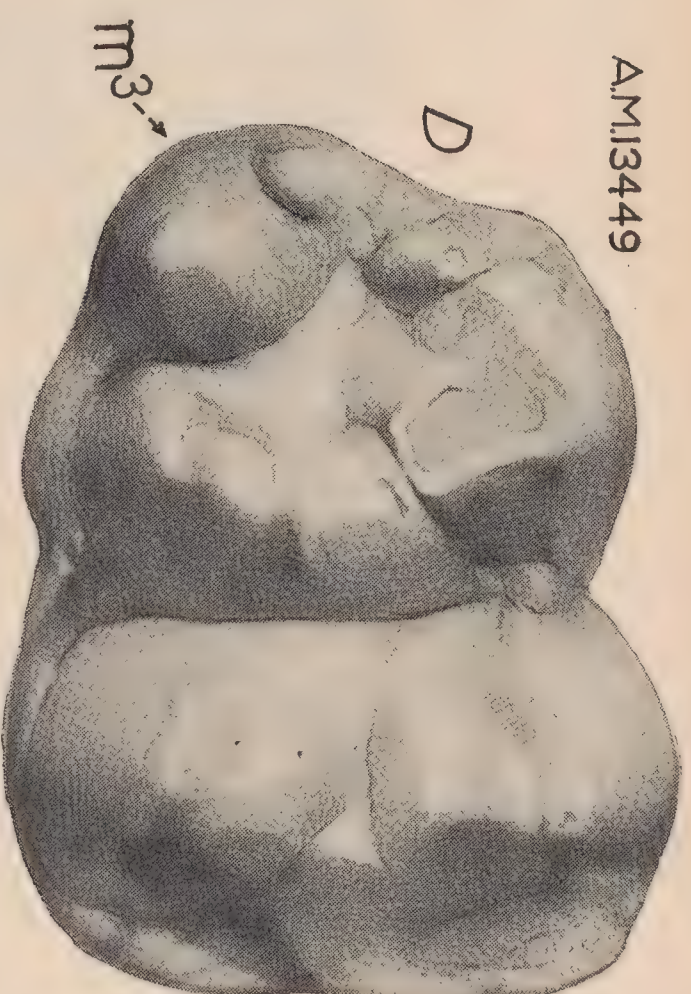
A.M. 15898 (cast)

A



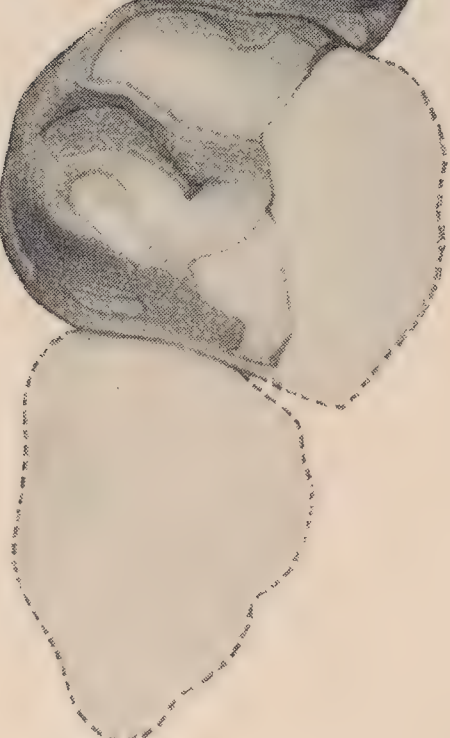
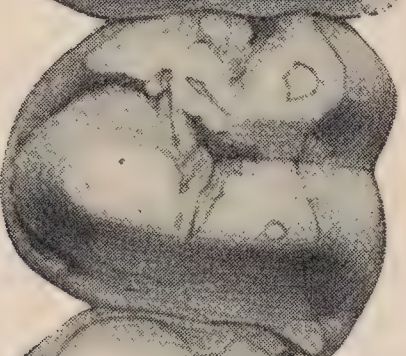
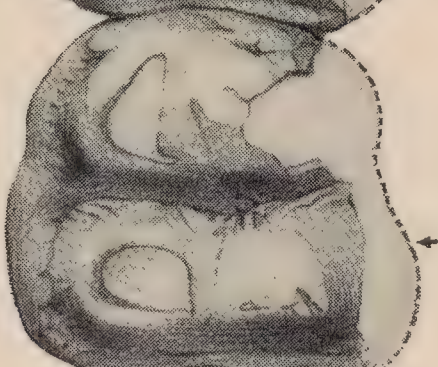
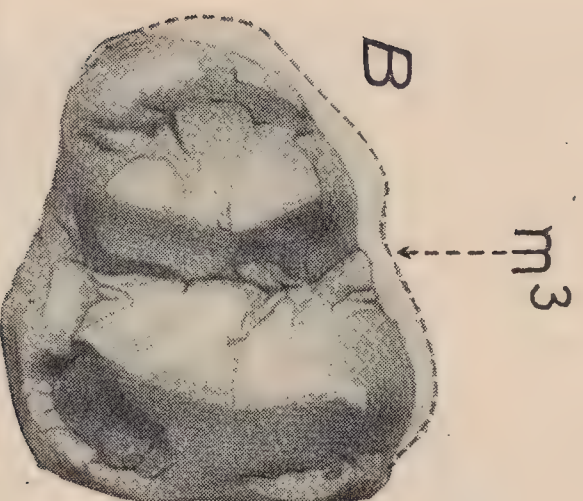
A.M. 13449

D



A.M. 13431

B



C



m2



E



A.M. 13437

Natural size.

A.M. 14547

Fig. 5.



crown. It is larger than that described by Schlosser, which seems likely to belong to *M. trigodon*. The upper tusks, viz. I<sup>2</sup>, of No. 13434 at hand measures about 140 mm. in straight length, 26 mm. and 29 mm. in the transverse and the antero-posterior diameter respectively, and about 38 mm. in the height of the fairly worn crown on the outer side. Andrews reported an upper tusk measuring 26 mm. in width from the Fluvio-marine Formation. It appears to coincide well with the present tusk in its width and seems to belong also to this species. Both the present and Andrew's specimens, representing tusks, are distinctly larger than one reported by Schlosser, which may probably belong to *M. trigodon*. The American Museum has one more tooth of extra-number from the Fluvio-marine Formation, which appears likely to represent a left third upper incisor of some species of *Mæritherium*. Its crown is triangular, with the anterior and posterior borders, as well as the internal basal cingulum, distinctly serrate; one of the serræ on either border is much more prominent than the others, appearing to represent the paracone on the anterior border and the metacone on the posterior border. It measures 14 mm. in length, 8 mm. in width and 13 mm. in the height of the crown. It is not clear at present whether this tooth might belong to *M. andrewsi* or *trigodon*. At any rate, all the three upper incisors of *Mæritherium* appear to have had the crown and root well differentiated. Further, Andrews reported two lower tusks, I<sub>2</sub>, one measuring 28 mm. and the other 20 mm. in width, from the Fluvio-marine Formation. The former seems likely to belong to the present species and the latter to *M. trigodon*.

|                |        | Lower Teeth |    |           |    | Upper Teeth |    |    |    |
|----------------|--------|-------------|----|-----------|----|-------------|----|----|----|
|                |        | No. 13437   |    | (Andrews) |    | (Andrews)   |    |    |    |
| P2             | length | 24          | .. | ..        | 26 | 27          | 25 | .. | 26 |
|                | width  | 11          | .. | ..        | 14 | 20          | 20 | .. | 22 |
| P3             | length | 29          | .. | 28        | 27 | 25          | 25 | 26 | 26 |
|                | width  | 17.5        | .. | 18        | 19 | 28          | 28 | .. | 32 |
| P4             | length | ....        | .. | 25        | 24 | 21          | 22 | 21 | 22 |
|                | width  | ....        | .. | 21        | 21 | 28          | 27 | .. | 29 |
| M1             | length | 29          | .. | 28        | 30 | 32          | 29 | 29 | 31 |
|                | width  | 21          | .. | 21        | 22 | 26          | 25 | .. | 27 |
| M2             | length | 32.5        | 33 | 34        | 32 | 32          | 33 | 32 | .. |
|                | width  | 26          | .. | 27        | 27 | 29          | 28 | .. | .. |
| M3             | length | 37          | 37 | ..        | 40 | ..          | .. | .. | .. |
|                | width  | 26          | 26 | ..        | 28 | ..          | .. | .. | .. |
| Length of P2-4 |        | 70          | .. | ..        | 73 | 73          | 70 | .. | 75 |
| Length of M1-3 |        | 100         | .. | ..        | 99 | ..          | .. | .. | .. |





Fig. 6. *Mæritherium trigodon* Andrews. Amer. Mus. No. 13430, skull.  
About one-fourth natural size. Superior view.

(4.) ***Mæritherium trigodon* Andrews**

*M. trigodon*.—ANDREWS, 1904, Geol. Mag., Decade 5, I, p. 112.

*M. trigonodon*.—ANDREWS, 1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt,' Brit. Mus., pp. 128–129, Pl. IX, fig. 5; SCHLOSSER, 1911, 'Beitr. z. Pal. u. Geol. Österreich-Ungarns, u. d. Orients,' XXIV, p. 130.



*M. lyonsi*—ANDREWS, 1906, 'Descr. Cat. Tert. Vert. Fayûm, Egypt,' Brit. Mus., pp. 128-129, *pars*, text-fig. 43, Pl. IX, fig. 3.

*M. andrewsi*.—SCHLOSSER, 1911, 'Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients,' XXIV, pp. 130-131, *pars*, Pl. XVI (VIII), figs. 6 and 7.

SPECIMENS.—No. 13430; greater part of a full-grown skull, bearing all the upper cheek-teeth *in situ*. No. 13431; fragment of a skull, including a greater part of a right half of palate, bearing  $P^3$ - $M^3$  *in situ*. No. 13433; left  $M^2$  attached to a fragment of upper jaw. No. 13435; fragment of a right ramus of mandible, with all the cheek-teeth *in situ*. No. 13436; fragment of a left ramus of mandible, with all the cheek-teeth *in situ*. No. 13439; right  $P_4$  and  $M_1$ , with their roots broken away. All from the Fluvio-marine Formation of Fayûm.

Andrews appears to have laid much weight upon the shape and structure of the posterior talon of  $M_3$  in distinguishing this species from his *M. lyonsi* (= *lyonsi* + *andrewsi*). As far as I can judge from the specimens in the American Museum and Andrews' statement and figures, such a character may not be adequate enough to be looked upon as specific; because, firstly, the posterior talon of  $M_3$  appears to be one of the most variable structures in the teeth of *Mærittherium* and, secondly, its appearance to the naked eye seems to differ according to the degree of age and of wearing of the tooth. The seeming difference according to the degree of age and of wearing of the tooth appears to hold true also as to the secondary tubercles between the principal ones of each lobe, as well as the basal cingulum of the molars.

The skull of No. 13430 measures 240 mm. in the length from the point at which the vertical plane tangential to the anterior borders of both  $P^2$  meets the median longitudinal line on the palate, to the basion, 145 mm. in the length from the same point to the median point of the posterior border of palate, about 180 mm. in the length from the anterior limit of the temporal vacuity in palatal view to the posterior lower border of squamosal, 42 mm. in the minimum width of the mid-cranial region (this dimension might be somewhat less than it ought to be in primary condition, as this part of this specimen appears to be crushed secondarily from side to side), 280 mm. in the zygomatic width, about 190 mm. in the distance between the upper borders of external auditory openings (including reliably restored parts to a slight extent), 220 mm. in the width of occiput, 91 mm. in the lateral extension of the two occipital condyles, 52 mm. in the width of palate between the two  $P^2$ , 34 mm. in the same between the two  $M^1$ , and about 150 mm. in the maximum height of the skull, including the upper cheek-teeth (including a restored part of sagittal crest to a slight extent). In this skull the sagittal and occipital



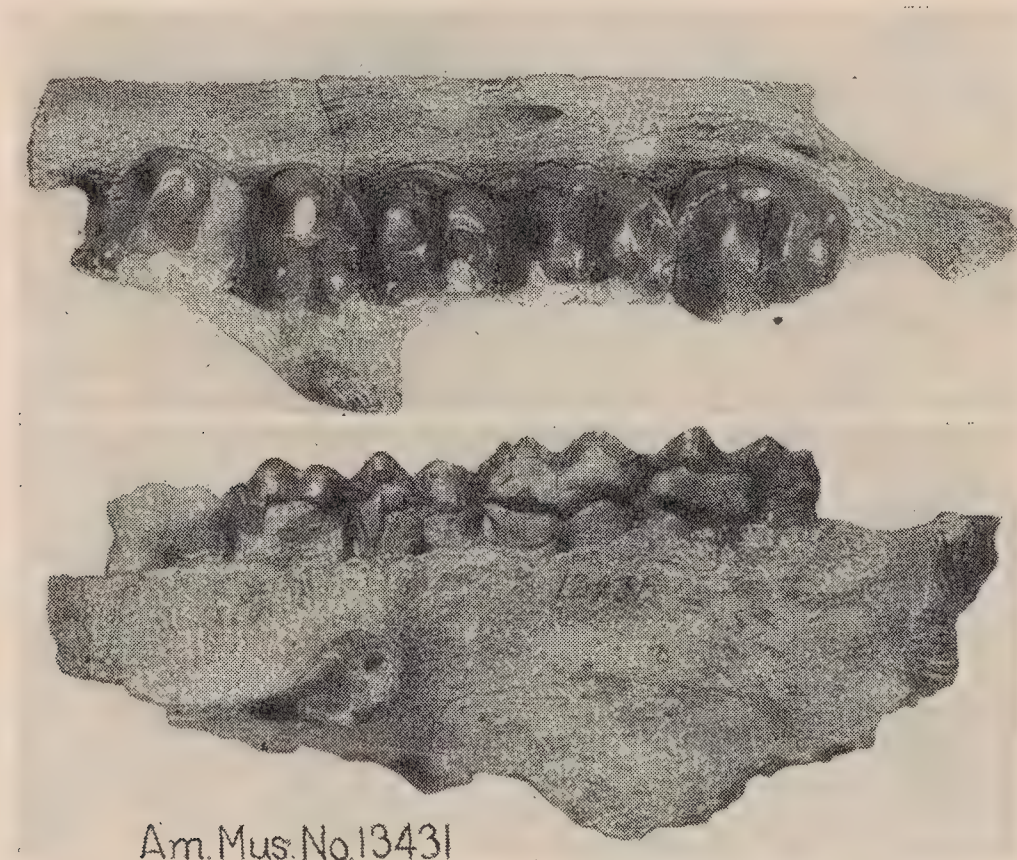


Am Mus No 13430

Fig. 7. *Mæriotherium trigodon* Andrews. Amer. Mus. No. 13430, skull.  
About one-fourth natural size. Lateral view, right side.



crests are extraordinarily well developed; and the occiput is strongly concave, so that its upper half, including the lambdoid crest, inclines distinctly backwards.



Am. Mus. No. 13431

Fig. 8. *Mæritherium trigodon* Andrews. Amer. Mus. No. 13431, right maxilla.

One-fourth natural size. Upper figure, occlusal view; lower figure, external view, right side.

The fragment of the skull of No. 13431 measures  $2 \times 19.5 = 39$  mm. in the width of palate between the two  $P^2$  (alveolus) and  $2 \times 15 = 30$  mm. in the same between the two  $M^1$ .

The mandibular ramus of No. 13435 measures 84 mm. in height at  $P_3$  without the tooth, and about 30 mm. in the length of diastema between  $I_2$  and  $P_2$  (including an estimated part to a slight extent). There are two anterior mental foramina on the outer surface of this ramus, one locating below the anterior lobe of  $P_3$  and the other below the middle part of  $P_4$ ; both the foramina are very small. A small but distinct foramen is present on the anterior surface of the ascending bar, just behind  $M_3$ . The mandibular ramus of No. 13436 measures about 73 mm. in height at  $P_3$  without the tooth. Two anterior mental foramina are observed to be present also in this ramus, one situated below the anterior lobe of  $P_3$  and the other below the anterior lobe of  $P_4$ .

Schlosser has pointed out that Andrews' specimen shown in his Pl. ix, fig. 3, under the name of *M. lyonsi* might refer to *M. trigodon*, though Schlosser himself has been inclined to look upon the last mentioned species as a female type of *M. andrewsi*. Again, Andrews' specimen shown in this text-fig. 43 seems to me to belong to *M. trigodon*.



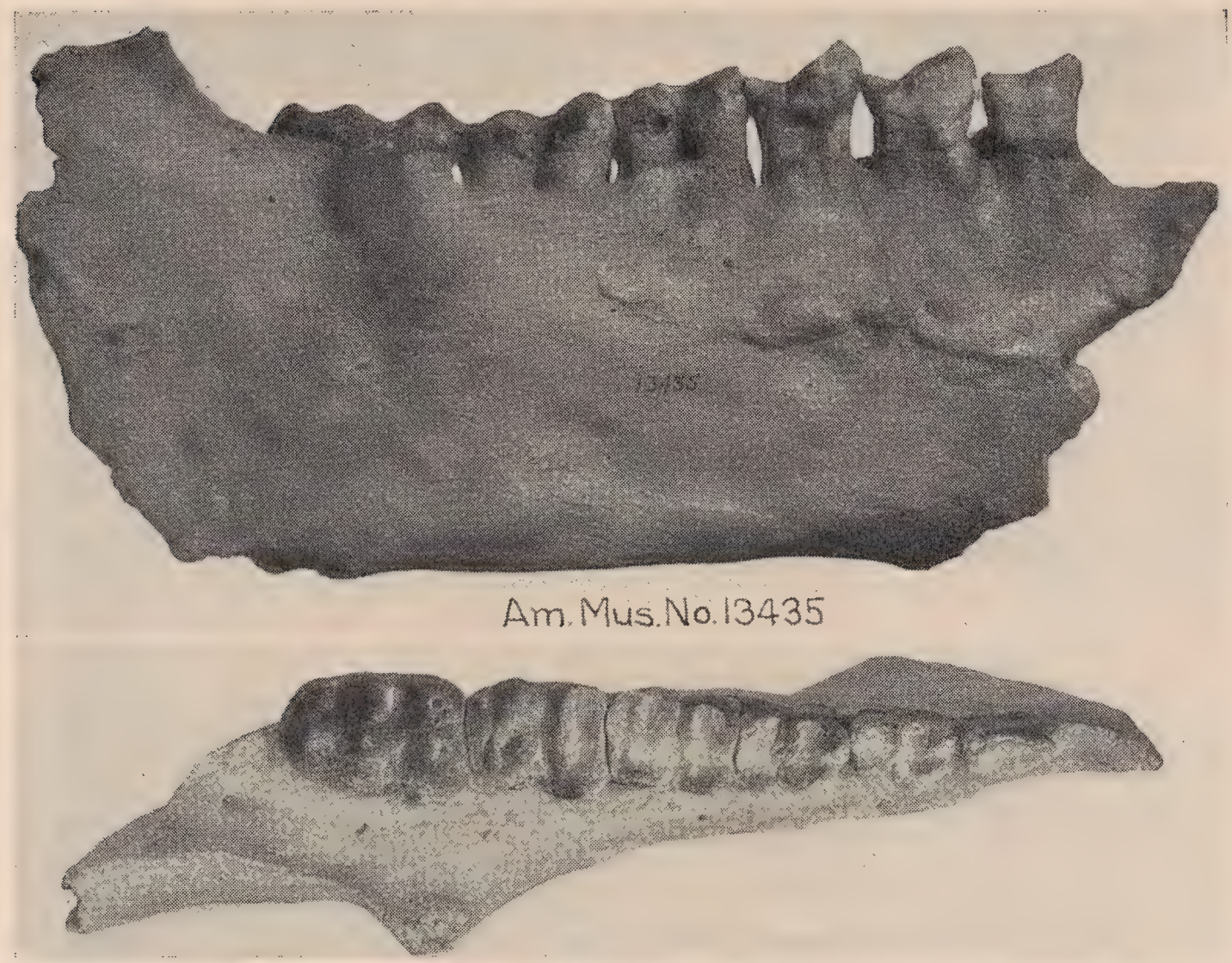


Fig. 9. *Mæritherium trigodon* Andrews. Amer. Mus. No. 13435, right ramus of mandible, incomplete.

One-fourth natural size. Upper figure, external view; lower figure, superior view.

The dimensions of the cheek-teeth of the specimens at hand, in comparison with those of Andrews', are tabulated as follows (in mm.):

|                |        | Lower Teeth  |              |              |           |    |    | Upper Teeth  |              |              |       |
|----------------|--------|--------------|--------------|--------------|-----------|----|----|--------------|--------------|--------------|-------|
|                |        | No.<br>13435 | No.<br>13436 | No.<br>13439 | (Andrews) |    |    | No.<br>13430 | No.<br>13431 | No.<br>13433 |       |
| P2             | length | 19.5         | 23?          | ..           | ..        | 23 | .. | right        | 19           | 22?          | ..... |
|                | width  | 10           | 11           | ..           | ..        | 11 | .. | left         | 21           | 18?          | ..... |
| P3             | length | 22           | 24?          | ..           | ..        | 25 | .. |              | 23           | 23.5         | 24    |
|                | width  | 15           | 14?          | ..           | ..        | 17 | .. |              | 26           | 24?          | 25?   |
| P4             | length | 23           | 23.5         | 25           | ..        | 24 | 22 |              | 20.5         | 20           | 22    |
|                | width  | 18           | 18.5         | 19           | ..        | 20 | .. |              | 24           | 23?          | 25.5  |
| M1             | length | 27           | 24           | 27.5         | 26        | .. | 27 |              | 25           | 22           | 24    |
|                | width  | 21           | 19           | 21           | ..        | .. | 21 |              | 25           | 26.5?        | 24    |
| M2             | length | 29           | 31           | ..           | 32        | .. | .. |              | 29           | 28           | 30    |
|                | width  | 24           | 24           | ..           | ..        | .. | .. |              | 28           | 27           | 25?   |
| M3             | length | 37           | 37           | ..           | 40        | .. | .. |              | 31           | 32           | 30    |
|                | width  | 26.5         | 25           | ..           | 24        | .. | .. |              | 26.5         | 27           | 26    |
| Length of P2-4 |        | 63           | 70           | ..           | ..        | 70 | .. |              | 60           | 63           | ..... |
| Length of M1-3 |        | 93           | 93           | ..           | 98        | .. | .. |              | 85           | 83           | 84    |



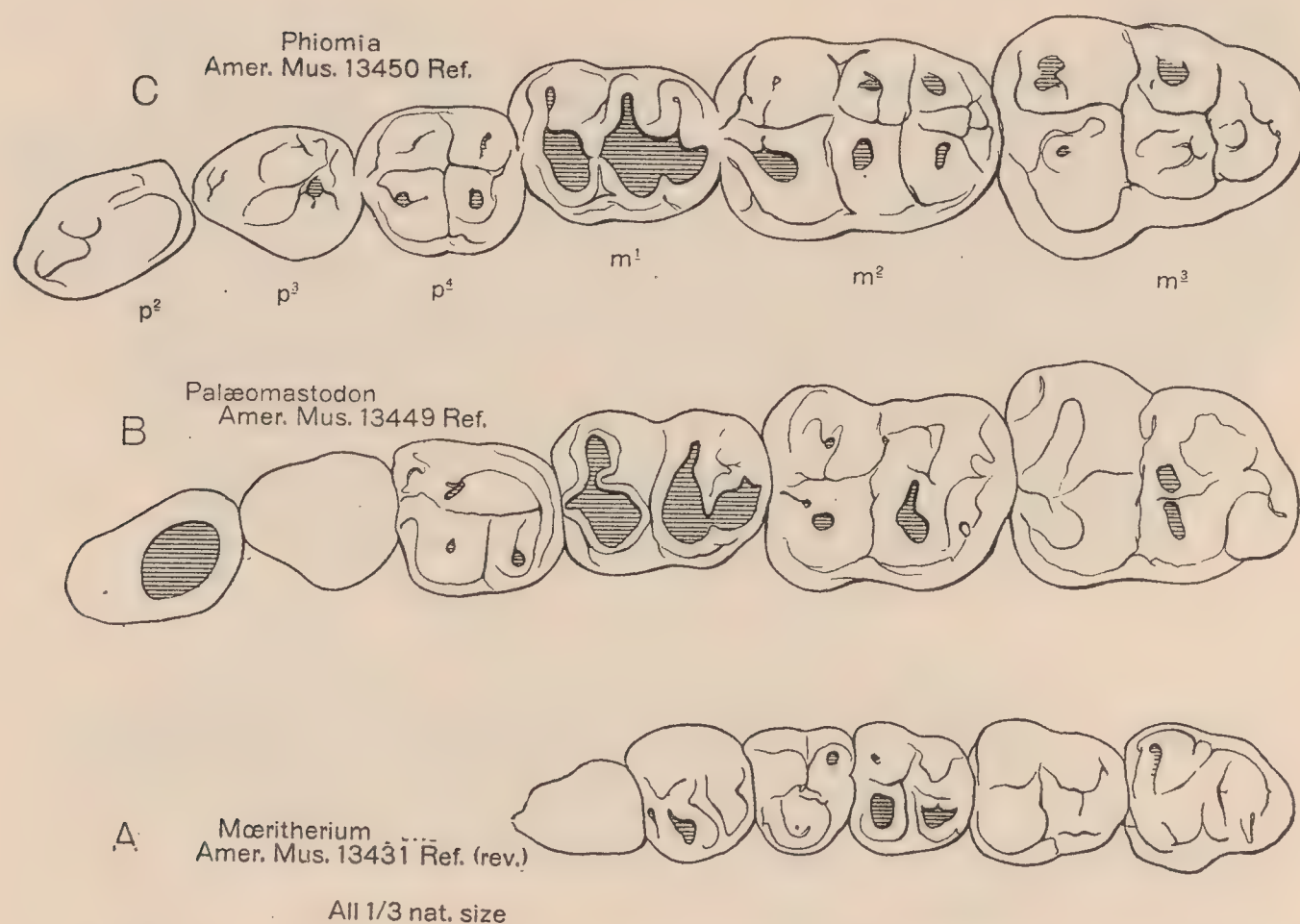


Fig. 10. *Mæritherium*, *Palæomastodon*, and *Phiomia*. Left upper grinding teeth. A, *Mæritherium*, Amer. Mus. No. 13431; B, *Palæomastodon*, Amer. Mus. No. 13449; C, *Phiomia*, Amer. Mus. No. 13450.

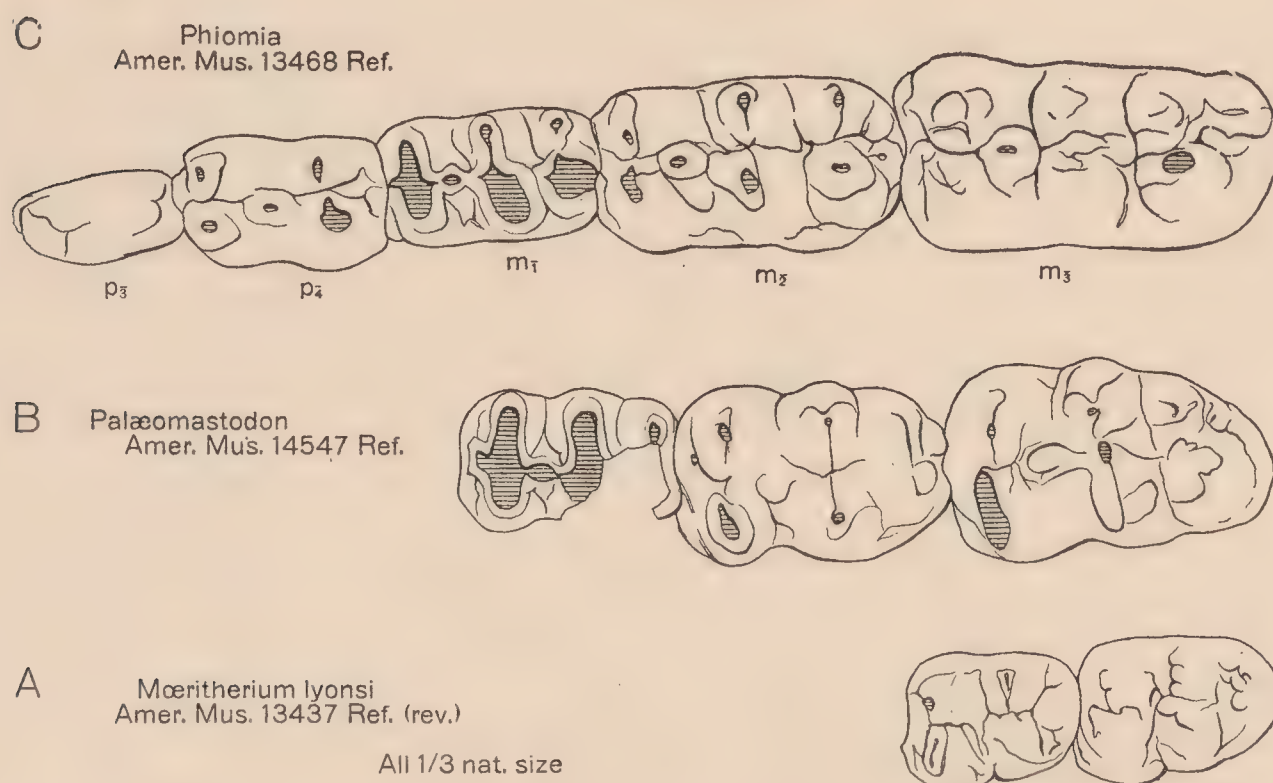


Fig. 11. *Mæritherium*, *Palæomastodon*, and *Phiomia*. Left lower grinding teeth. A, *Mæritherium lyonsi* Andrews, Amer. Mus. No. 13437 (reversed), second and third lower molars; B, *Palæomastodon*, Amer. Mus. No. 14547, first, second and third lower molars; C, *Phiomia*, Amer. Mus. No. 13468.



As already stated, one of Andrews' specimens from the Fluvio-marine Formation, representing a lower tusk, I<sub>2</sub>, which measures 20 mm. in width, may belong to this species. Schlosser's specimen, representing a fragment of an upper jaw with I<sup>1</sup> and I<sup>2</sup>, which measures 14 mm. and 21 mm. in width respectively, may probably refer to this species, also as already cited.

SUMMARY OF THE SYSTEMATIC PART

I have now reviewed the four species of *Mæritherium* and discussed their mutual relationship. The ranges of the hitherto known dimensions of the tusks and cheek-teeth of these four species may be tabulated (in mm.) as follows:

| Lower Teeth                |               |                |                 |                 |
|----------------------------|---------------|----------------|-----------------|-----------------|
|                            | <i>lyonsi</i> | <i>gracile</i> | <i>andrewsi</i> | <i>trigodon</i> |
| P <sub>2</sub> { length    | 22            |                | 24— 26          | 19.5—23         |
| width                      | 16            |                | 11— 14          | 10—11           |
| P <sub>3</sub> { length    | 23            | 22             | 27— 29          | 22—25           |
| width                      | 21            | 15             | 17.5— 19        | 14?—17          |
| P <sub>4</sub> { length    | 25            | 21             | 24— 25          | 22—25           |
| width                      | 23            | 18             | 21              | 18—20           |
| M <sub>1</sub> { length    | 26.5          | 22—23          | 28— 30          | 24—27.5         |
| width                      | 24.5          | 19—20          | 21— 22          | 19—21           |
| M <sub>2</sub> { length    | 28—35         | 27—28          | 32— 34          | 29—32           |
| width                      | 25—30         | 22—23          | 26— 27          | 24              |
| M <sub>3</sub> { length    | 39—42         | 33—34          | 37— 40          | 37—40           |
| width                      | 28—30         | 24             | 26— 28          | 24—26.5         |
| Length of P <sub>2-4</sub> | 69+           | 63+            | 70— 73          | 63±70           |
| Length M <sub>1-3</sub>    | 140+          | 84             | 99—100          | 93—98           |
| Width of I <sub>2</sub>    |               | 20+            | 28              | 20              |

| Upper Teeth                |               |                |                 |                 |
|----------------------------|---------------|----------------|-----------------|-----------------|
|                            | <i>lyonsi</i> | <i>gracile</i> | <i>andrewsi</i> | <i>trigodon</i> |
| P <sup>2</sup> { length    | 27            | 22             | 25—27           | 19—22?          |
| width                      | 23?           | 18             | 20—22           | 18?—21          |
| P <sup>3</sup> { length    | 26.5          | 20             | 25—26           | 23—24           |
| width                      | 29.5          | 23             | 28—32           | 24?—26          |
| P <sup>4</sup> { length    | 23            | 20             | 21—22           | 20—22           |
| width                      | 27.5          | 21?            | 27—29           | 23?—25.5        |
| M <sup>1</sup> { length    | 29            | 23—25          | 29—32           | 22—25           |
| width                      | 27            | 21—23          | 25—27           | 24—26.5         |
| M <sup>2</sup> { length    | 26?—30        | 24—27          | 32—33           | 28—30           |
| width                      | 23.5—28       | 23—25          | 28—29           | 24—28           |
| M <sup>3</sup> { length    | 32—37±        | 28             |                 | 30—32           |
| width                      | 28—30±        | 24—25          |                 | 26—27           |
| Length of P <sup>2-4</sup> | 67—68         | 62             | 70—75           | 60—63           |
| Length M <sup>1-3</sup>    | 85            | 75—79±         |                 | 83—85           |
| Width of I <sup>2</sup>    | 28            |                | 26              | 21              |



As far as judged from the absolute and relative dimensions of the cheek-teeth, *M. andrewsi* and *trigodon* appear to be more closely allied with each other than are *M. lyonsi* and *gracile*. And, as far as judged from the relative dimensions of the lower cheek-teeth, *M. gracile* appears to be more closely allied with *M. andrewsi* and *trigodon* than *M. lyonsi* does to the same. Consequently, *M. lyonsi* and *gracile* appear not to be sexual dimorphic types of one and the same species, and *M. andrewsi* and *trigodon* appear so also. Moreover, it appears to be more probable that *M. gracile* might be an ancestral type of both *M. andrewsi* and *trigodon* than that *M. lyonsi* and *gracile* might be ancestral types of *M. andrewsi* and *trigodon* respectively.



**Article V.—THE ILIUM IN DINOSAURS AND BIRDS**

BY ALFRED S. ROMER

In both great groups of dinosaurs and in birds are found anterior prolongations of the ilium not present in primitive reptiles. The possession of a preacetabular part of the ilium is often used as a diagnostic character of the Dinosauria, but, when considered in connection with the related musculature, it is evident that these processes differ greatly, morphologically and functionally, in the two orders of dinosaurs and that they have probably had independent histories. Further, while the pars preacetabularis ilii of the bird may be considered as a development of that of the Ornithischia, it differs from it to a marked degree.

As shown in a previous paper<sup>1</sup> the anterior edge of the primitive ilium ascended vertically from the acetabulum, often with a slight projection at the top as an anterior superior spine. This marked the anterior termination of the ilio-tibial muscle or muscles, and the attachment of the ilio-pubic ligament and the adjacent axial muscles.

In the Saurischia, the pars preacetabularis is an anterior extension of the whole iliac surface, which now runs forward beyond the level of the acetabulum and in late forms arches outward considerably. The spine is not evident; the forward growth of the iliac blade has extended to or beyond the point at which it terminated and has incorporated it in the dorsal edge of the blade.

The pars preacetabularis in the Ornithischia is in marked contrast to this. It is a long, finger-like projection, a greatly exaggerated spine, which extends forward not the external surface of the ilium but merely its dorsal border which terminated at the spine. It extends more dorsally and medially than that of the Saurischia.

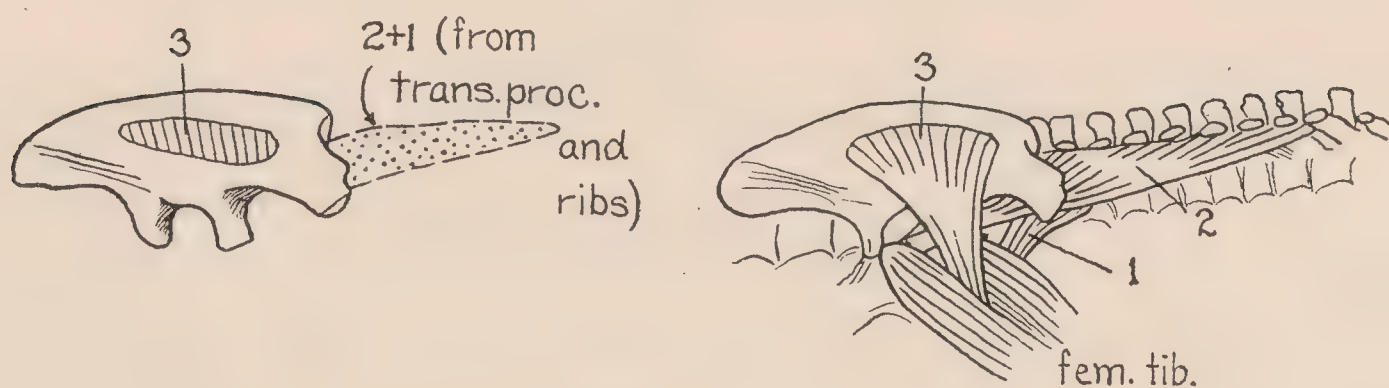
These two types are well differentiated even in the Trias. They are apparently independent developments, along different lines, from the anterior edge of the primitive ilium.

From other features of the pelvic structure we may infer that the pars preacetabularis of birds is homologous with that in the Ornithischia, but they differ considerably and we have no forms to bridge the gap; the *Archæopteryx* ilium is here shaped as in later birds. In order to attain this condition from that found in Ornithischia, we must assume that the ornithischian pars preacetabularis has swung medially, fused with verte-

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<sup>1</sup>A. S. Romer, 1922 Bull. Amer. Mus. Nat. Hist., XLVI, Pl. XLIV.

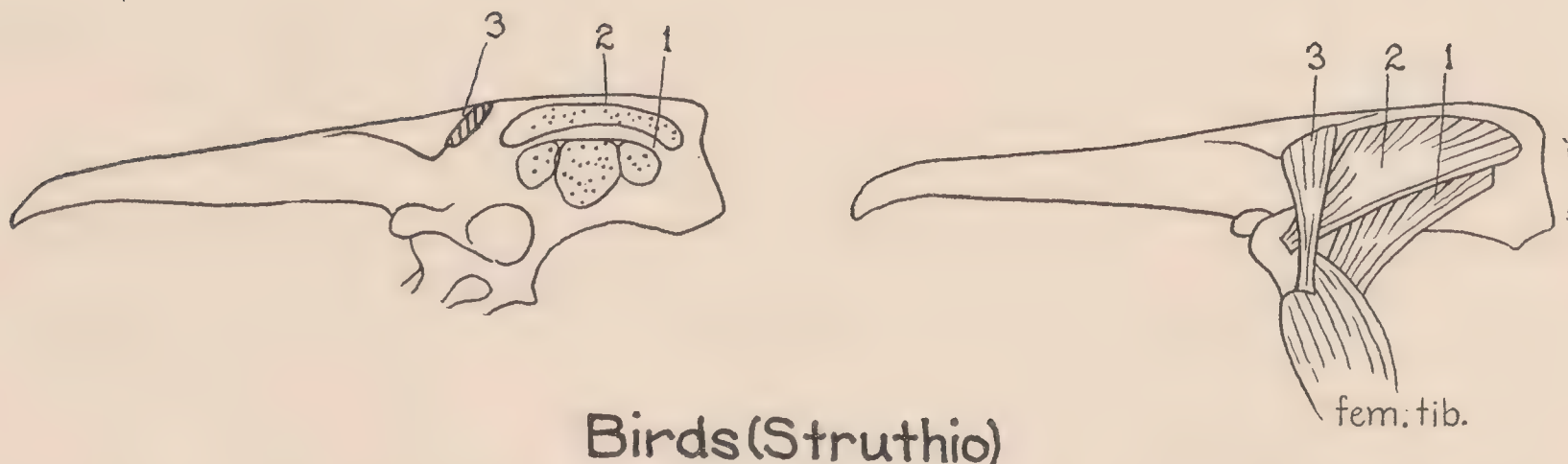




### Saurischians (Tyrannosaurus)



### Ornithischians (Corythosaurus)



### Birds (Struthio)

Fig. 1. The ilium (left) and its deeper musculature (right) in the two dinosaurian orders and birds, to show the contrast in the preacetabular parts.

In all cases the long extensors to the tibia extend along the upper border. The ilio-femoralis (3) probably originated from the outer surface, including the preacetabular extension in the Saurischia, but in Ornithischia, as in birds, became confined to the crest above the acetabulum. The pubo-ischio-femoralis internus, including the "quadratus lumborum" (1-2) undoubtedly ran beneath the saurischian process. In Ornithischia this process was primitively for the ilio-tibial muscles, a finger-like prolongation of the anterior spine contrasting markedly with that of the Saurischia. In later forms it began to pick up the origin of this muscle, a process which has been completely accomplished in birds, resulting in the large pars preacetabularis of that group, closely applied to the original lumbar region.

tebræ that were originally presacral to form a new anterior portion of the sacrum, and built up a broad surface below its original extent.

The musculature may now be considered.



**ILIO-TIBIALIS.** This muscle (sometimes in several parts) usually arises tendinously from the dorsal edge of the ilium. The possession of the ilio-tibialis origin at the dorsal edge is the one common feature of the pars preacetabularis in the groups discussed. In the Saurischia, its presence on the process was probably incidental; in the Ornithischia, the anterior prolongation of its area of origin appears to have been the main function of the process. It occupies this same position in birds, although a new function of the process has been added by the development of the surface ventral to its area of origin.

**ILIO-FEMORALIS.** This primitively occupies a muscular area of origin above and rather to the back of the acetabulum. In the Saurischia the anterior expansion of the external iliac surface apparently has allowed the muscle to expand anteriorly. In the Ornithischia, the iliac surface tends to grow smaller rather than larger, and probably the muscle was reduced in its area of origin and very likely in bulk. In accordance with this, the probable bird homologue of this muscle, the ilio-femoralis externus is rather small and has a tendinous origin from the crest of the ilium above the acetabulum.

**PUBO-ISCHIO-FEMORALIS INTERNUS.** This muscle primitively arises from the inner surface of the pubo-ischium and inserts, as in lizards (Fig. 2), in two areas on the femur, one on the anterior (medial) aspect of the shaft, the other dorsally, close to the head. In the Alligator, part III of pubo-ischio-femoralis internus of Gadow<sup>1</sup> occupies the first primitive area of insertion; the second is occupied with a muscle which that writer calls "quadratus lumborum," but which is obviously a part of pubo-ischio-femoralis internus.

Both these parts arise dorsally, as contrasted with the original ventral internal position of the muscle's origin. This, in connection with the fact that there is no muscle in birds which corresponds in its origin with that of the primitive pubo-ischio-femoralis internus, suggests that this dorsal migration is a common archosaurian character.

The position, and sometimes the arched shape, of the saurischian preacetabular process indicates that this muscle arose in this group from the lumbar region, as in the Crocodilia, and passed outward beneath the process, with which it was unconnected.

The ornithischian process also evidently had nothing to do, primitively, with this muscle, which here also passed beneath the anterior prolongation of the ilium in its passage from the lumbar vertebræ to the

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<sup>1</sup>Gadow's parts I and II are probably not part of the true pubo-ischio-femoralis internus; their homologies are not essential to the point in question and will be discussed at another time.



femur. In late members of the order such an association probably took place to a certain extent.

But it will be noted that in birds this process has swung inwards to the region of origin of the pubo-ischio-femoralis internus from the lumbar vertebræ and, having fused with the vertebræ to form a new portion of the sacrum, has built a broad surface of bone over the former area of origin of the muscle. We would expect that the muscles arising from this surface then, to be the avian homologues of the pubo-ischio-femoralis internus. Their areas of insertion and general relations bear this out (Fig. 1).

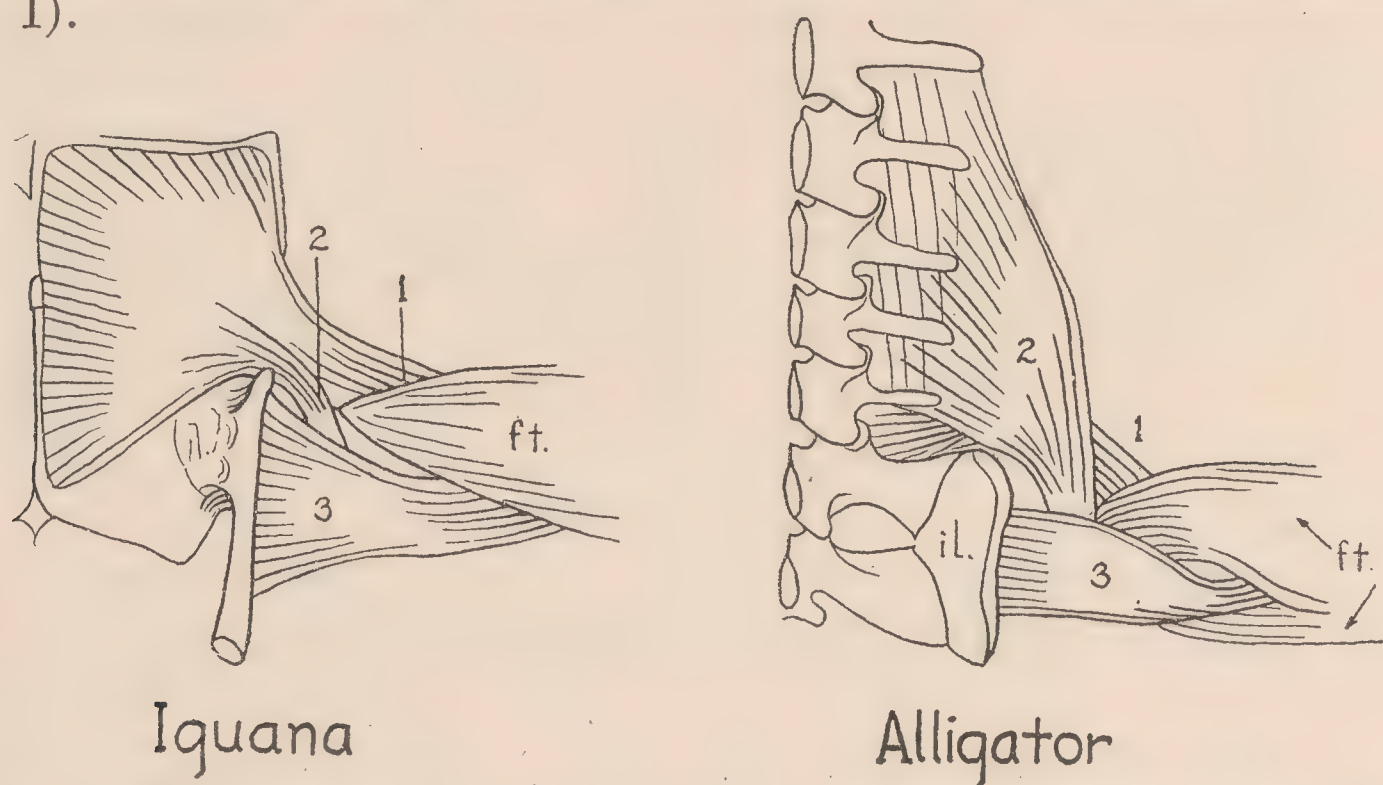


Fig. 2. Dorsal views of pelvic muscles in *Iguana* and Alligator (the sacrum removed in *Iguana*).

A part of the pubo-ischio-femoralis internus of *Iguana* (1) inserts anteriorly, as does part of the muscle similarly named by Gadow in the alligator. Another part (2) inserts similarly to the muscle named 'quadratus lumborum' in the alligator. The position of ilio-femoralis (3) should be noted and the muscles compared with the lateral views in Fig. 1.

Superficially, the preacetabular portions of the ilium in birds and saurischian dinosaurs appear somewhat alike; but it has been seen that they lie on opposite sides of the pubo-ischio-femoralis internus. The bird pars preacetabularis can, however, as we have seen, be derived from that found in the Ornithischia. And further, this process probably evolved independently of that found in the Saurischia.

I wish to express my thanks to Dr. W. K. Gregory, with whom this matter was discussed, for many valuable criticisms.

#### SUMMARY

1. The saurischian pars preacetabularis ilii is an extension of the external iliac surface.

2. The ornithischian pars preacetabularis is an exaggeration of the anterior iliac spine.



3. The bird pars preacetabularis may have been derived from that of the Ornithischia by a movement medially and the building up of a surface ventral to the original process.

4. The saurischian pars preacetabularis passed dorsal to the puboischio-femoralis internus. That of the Ornithischia did so primitively but later picked up a portion of its origin. In the birds the entire origin of the muscle is from the pars preacetabularis, which is now medial to the muscle, in strong contrast to the saurischian process, which is lateral to it.







**Article VI.—ECHINODERMS FROM LOWER CALIFORNIA,  
WITH DESCRIPTIONS OF NEW SPECIES: SUPPLEMEN-  
TARY REPORT<sup>1</sup>**

BY HUBERT LYMAN CLARK

Museum of Comparative Zoölogy, Cambridge, Massachusetts

When the collection of echinoderms made by the 'Albatross' Expedition to Lower California in the spring of 1911 was sent to me about ten years ago, by some mistake a considerable amount of material was not shipped. This was discovered and sent to me in the late fall of 1921 and, as it contains species not in the original lot, it seems desirable to publish this supplementary report.<sup>2</sup>

This second collection contains 462 specimens of 58 species, and no fewer than ten of these species were not represented in the first collection. Moreover, two of the ten additional species are new to science, though unfortunately each is represented by only a single broken specimen. The entire collection of echinoderms made by the 'Albatross' on her Lower California cruise, therefore, consisted of 2343 specimens of 117 species, of which nine were undescribed. There were 41 kinds of sea-stars, 34 of brittle-stars, 21 of echini and 20 holothurians, and a single specimen, in the supplementary collection, represents the comatulids or feather-stars. The presence of this comatulid, which is of an undescribed species, is perhaps the most interesting feature of the additional material.

More than a third of this second collection is from shore stations, of which San Francisquito Bay is easily the most important, 98 specimens of 10 species coming from there, two of these not being in the first collection. It is interesting to note that the remarkable new brittle-star, described beyond, was taken at Station 5694, which was noted in my first report as being the station where the most species were taken. Here, at a depth of 640 fms., no fewer than 19 species were collected. The new comatulid is from Station 5692, which is off Point San Tomas, west coast of Lower California, a region noted in my earlier report for the large number of species found there.

I desire to express here my thanks to Mr. Roy W. Miner, of The American Museum of Natural History, for courtesies in connection with the preparation of the present report.

<sup>1</sup>Scientific Results of the Expedition to the Gulf of California in charge of Dr. C. H. Townsend, by the U. S. Fisheries Steamship 'Albatross' in 1911; Commander G. H. Burrage, U. S. N., Commanding. XII. Published by permission of the U. S. Commissioner of Fisheries.

<sup>2</sup>The present report is supplementary to 'Echinoderms from Lower California, with descriptions of new species.' By Hubert Lyman Clark, 1913, Bull. Amer. Mus. Nat. Hist., XXXII, pp. 185-236, Pls. XLIV-XLVI.



## CRINOIDEA

**Trichometra europacifica**, new species

Centro-dorsal relatively large, conical, covered by the cirrus sockets, which are arranged in about three horizontal series, no vertical series or radial groups being indicated.

Cirri about 20 in number, 4 or 5 mm. long, with 15 or 16 segments. The cirri at the apex of the centro-dorsal are noticeably smaller than those in the outer or marginal series. Basal segment almost discoidal, its length not one-half its thickness; second segment not quite so long as wide; third, distinctly longer than its distal diameter, which is greater than the proximal; fourth segment the longest of all, twice as long as the distal diameter, which is much greater than the proximal; the segment is nearly cylindrical where its diameter is least, proximal to the middle; the distal margin is flaring, especially on the dorsal side, where it projects considerably. Fifth segment very similar to fourth, but sixth and seventh are shorter and stouter. Succeeding segments each a trifle shorter and smaller than its predecessor, and the least diameter is at the proximal margin more and more clearly. But even the fifteenth and sixteenth segments are longer than their distal diameter. Sixteenth segment with a conspicuous opposing spine which is not quite so long as the diameter of the segment. Terminal claw moderately slender, slightly curved, about equal to the last segment in length.

Radials almost bowl-shaped, the width nearly three times the length in the median line, which is somewhat less than the lateral margins, as the distal margin is distinctly concave. The first costals are similar to the radials but are lower, the width being fully three times the length. Costal axillaries rhombic, about as long as broad, the margins slightly concave, the angles blunt and rounded; the anterior margins are swollen, flaring and a little roughened. Surface of all the I Br series otherwise quite smooth. Costals and axillaries scarcely in contact, but first brachials externally appressed; hence there is a distinct pit-like depression between the I Br series of adjoining radii.

Ten arms, all broken distally so the length can only be estimated; probably about 25 mm. long. First brachial short, its outer edge about twice as long as inner, its distal margin only a little concave and not at all flaring, and nearly smooth; second brachial irregularly pentagonal, about as long as thick; third and fourth brachials, united by syzygy, together longer than the second and therefore distinctly longer than broad; following brachials about as long as broad, except syzygial pairs, which distally probably occur at intervals of two bifascial articulations. Beyond the third brachial, the distal margin of each pinnule-bearing segment projects as a spiny knob, characteristic of the genus, but these knobs are not conspicuous and are best seen in a perfectly profile view of a dried arm; when thus viewed the dorsal median line of each brachial is distinctly concave.

Pinnules all broken and defective, but enough segments are left to show that all were very slender and distally filiform. In the first pinnule the basal joint is about as long as wide, the second is longer, the third still longer and the fourth is fully twice as long as thick. The distal segments on all the pinnules are extremely slender at middle, but conspicuously swollen at the joints. Genital glands are present on some of the basal pinnules.

Color very pale brown dorsally, the cirri nearly white; oral surface dark brown.

TYPE.—Cat. No. —, U. S. Nat. Mus., from Station 5692.



Station 5692. Off Pt. San Tomas, west coast of Lower California, 1076 fms. Bottom temp. 37.1°.

One specimen.

Owing to the locality and the fact that there was only a single small broken specimen, I was inclined to list this comatulid as *Thaumatometra parvula* (Hartlaub), in spite of the obviously different cirri, but Mr. Austin H. Clark suggested to me that the arms were evidently the arms of a *Trichometra* and the combination of characters shown by the cirri, pinnules, and arms clearly indicated an undescribed species. Oddly enough, the species most closely resembling this new one from the eastern Pacific is the little *Trichometra minutissima* A. H. Clark, from off the Brazilian coast in 818 fms. But the Atlantic species has a very different centro-dorsal, far more numerous cirri, much rougher costals and somewhat more slender pinnules. For convenience in comparing the two species, I have modeled my description of *europacifica* after the pattern of the original description of *minutissima* (1908, Proc. U. S. Nat. Mus., XXXIV, p. 233).

#### ASTEROIDEA

##### *Astropecten erinaceus* Gray

*Astropecten erinaceus* GRAY, 1840, Mag. Nat. Hist., (new series), VI, p. 182.

The present specimens are large,  $R=80$  and 125 mm., and are conspicuously spiny. The color is the usual yellow-brown of dry sea-stars. In the larger specimen,  $r$  and  $br$  each = 28 mm. and hence  $R=4.5 r$ .

Conception Bay, east coast of Lower California.

Two specimens.

##### *Thrissacanthias penicillatus* (Fisher)

*Persephonaster penicillatus* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 297.

*Thrissacanthias penicillatus* FISHER, 1910, Ann. Mag. Nat. Hist., (8) V, p. 171.

These specimens are large adults, ranging from  $R=100$  mm. to  $R=225$  mm., and call for no special comment. They are merely additional specimens from four stations previously recorded, namely Stations 5694, 5697, 5698, and 5699.

Thirteen specimens.

##### *Pectinaster agassizii* (Ludwig)

*Cheiraster agassizii* LUDWIG, 1905, Mem. Mus. Comp. Zoöl., XXXII, p. 1.

*Pectinaster agassizii* LUDWIG, 1910, Sitz. K. Preuss. Akad. Wiss., XXIII, p. 449.

These specimens range in length of  $R$  from 15 to 55 mm. They are in part from Stations 5689 and 5692, whence they were previously



recorded, but there are 18 specimens from Station 5696. Off San Luis Obispo County, California, 440 fms. Bottom temp., 39.9°.

Forty-four specimens.

**Nearchaster aciculosus** (Fisher)

*Acantharchaster aciculosus* FISHER, 1910, Zool. Anz., XXV, p. 550.

*Nearchaster aciculosus* FISHER, 1911, Ann. Mag. Nat. Hist., (8) VII, p. 92.

These are simply five additional adult specimens from Station 5694. The length of R ranges from 90 to 150 mm.

**Pseudarchaster pusillus** Fisher

*Pseudarchaster pusillus* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 304.

This is merely additional material from Station 5675. There are 18 specimens with R = 28 to 33 mm.

**Ceramaster leptoceramus** (Fisher)

*Tosia leptocerama* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 306.

*Ceramaster leptoceramus* FISHER, 1911, Bull. U. S. Nat. Mus., No. 76, p. 210.

There are two additional specimens from Station 5675 with R = 35 to 40 mm. They seem to me more like *japonicus* than *leptoceramus*, except for the presence of abactinal radial secondary plates.

**Oreaster occidentalis** Verrill

*Oreaster occidentalis* VERRILL, 1867, Trans. Connecticut Acad. Sci., I, p. 278.

The present large series shows great diversity in the number, distribution, and acuteness of the abactinal spines and the tubercles. The five radial spines near margin of disk are usually, but not always, conspicuous. A perfectly preserved specimen, which seems to have retained the living form very well, has R = 80 mm., r = 35 mm., br = 25 mm. and vertical diameter of disk = 45 mm. Hence  $R = 2.3r$ ,  $3br$ , and only 1.3 v.d. None of the specimens give any clue as to the color in life. The largest specimens have R = 105 mm.

San Francisquito Bay, east coast of Lower California. Carman Island, east coast of Lower California.

Thirty-two specimens.

**Amphiaster insignis** Verrill

*Amphiaster insignis* VERRILL, 1868, Trans. Connecticut Acad. Sci., I, p. 373.

There is a single small specimen, with R = only 30 mm., from Conception Bay, east coast of Lower California.



**Phataria unifascialis** (Gray)

*Linckia* (*Phataria*) *unifascialis* GRAY, 1840, Mag. Nat. Hist., (new series), VI, p. 285.

*Phataria unifascialis*, SLADEN, 1889, 'Rep. Voy. 'Challenger,' Zoöl.,' XXX, p. 786.

These dried specimens from two additional localities have  $R = 55$  to 80 mm.

Espiritu Santo Island, east coast of Lower California.

San Francisquito Bay, east coast of Lower California.

Twelve specimens.

**Pharia pyramidata** (Gray)

*Ophidiaster* (*Pharia*) *pyramidatus* GRAY, 1840, Mag. Nat. Hist., (new series), VI, p. 284.

*Pharia pyramidata* SLADEN, 1889, 'Rep. Voy. 'Challenger,' Zoöl.,' XXX, p. 784.

This well-known and characteristic "West coast" species was not represented in the first collection, but now there are some small specimens at hand, with  $R = 67$  to 74 mm.

San Francisquito Bay, east coast of Lower California.

Three specimens.

**Solaster borealis** (Fisher)

*Crossaster borealis* FISHER, 1906, Proc. Washington Acad. Sci., VIII, p. 134.

*Solaster borealis* FISHER, 1911, Bull. U. S. Nat. Mus., No. 76, p. 320.

There is an additional specimen from Station 5694, with 11 rays,  $R = 30$  mm., and another from Station 5696, with 11 rays,  $R = 50$  mm.

**Heterozonias alternatus** (Fisher)

*Crossaster alternatus* FISHER, 1906, Proc. Washington Acad. Sci., VIII, p. 131.

*Heterozonias alternatus* FISHER, 1910, Ann. Mag. Nat. Hist., (8) V, p. 172.

Considerable additional material of this species is at hand from Stations 5694, 5697, and 5698. They show a good range in size, as  $R = 23$  to 110 mm. One specimen has eleven rays; all the others ten.

Fourteen specimens.

**Lophaster furcilliger** Fisher

*Lophaster furcilliger* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 312.

There are ten more specimens of this sea-star from Station 5694, with  $R$  ranging from 27 to 60 mm.

**Peribolaster biserialis** Fisher

*Peribolaster biserialis* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 313.

There is another specimen from Station 5696, and it is the largest of those taken, as  $R = 20$  mm.



**Hymenaster perissonotus** Fisher

*Hymenaster perissonotus* FISHER, 1910, Ann. Mag. Nat. Hist., (8) V, p. 170.

Two specimens from Station 5691 are much larger than those of the first collection, as  $R$  = about 60 mm.

**Zoroaster evermanni** Fisher

*Zoroaster evermanni* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 317.

There are three specimens from Station 5699 with  $R$  = 135 to 152 mm. One has the big pedicellariæ characteristic of Fisher's subspecies *mordax*, but these are lacking in the other two. It is worth noting that the locality is on the border line, both geographically and bathymetrically, of the range of the subspecies.

**Zoroaster ophiurus** Fisher

*Zoroaster ophiurus* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 315.

There are three additional specimens of this species from Station 5689, with  $R$  = 125 to 140 mm.

**Myxoderma platyacanthum** (H. L. Clark)

*Zoroaster platyacanthus* H. L. CLARK, 1913, Bull. American Mus. Nat. Hist., XXXII, p. 199.

*Myxoderma platyacanthum* FISHER, 1919, Ann. Mag. Nat. Hist., (9) III, p. 393.

There are three additional specimens in the present collection, with  $R$  = 60 to 70 mm. They bear the label "D 5695. Mar. 15, 1911." This is clearly a mistake as the station number and date do not correspond. It is evident that these specimens are from the type locality, Station 5675, where collecting was done on March 15.

Fisher's further investigations into the anatomy of the Zoroasteridæ have established the generic rank of *Myxoderma* and have shown that the present species belongs in the genus.

**Myxoderma sacculatum** (Fisher)

*Zoroaster (Myxoderma) sacculatus* FISHER, 1905, Bull. U. S. Bur. Fish., XXIV, p. 316.

*Myxoderma sacculatum* FISHER, 1919, Ann. Mag. Nat. Hist., (9) III, p. 392.

This species is not recorded as in the first collection. There are five specimens from Station 5694, having  $R$  = 180 to 185 mm.

**Heliaster kubiniji** Xantus

*Heliaster kubiniji* XANTUS, 1860, Proc. Acad. Nat. Sci. Philadelphia, p. 568.

In the present series of very poorly preserved specimens, there is great range in size, as  $R$  = 13 to 100 mm. The number of rays ranges



from 15 to 24, but all the large specimens have 23. There is one with 15 rays, one with 17, one with 19, one with 20, five with 21, five with 22, eight with 23, and one with 24.

Espiritu Santo.

San Francisquito Bay, east coast of Lower California.

Twenty-four specimens.

### ***Asterias forreri* De Loriol**

*Asterias forreri* DE LORIO, 1887, Rec. Zool. Suisse, IV, p. 401.

There is a very poorly preserved sea-star in the present collection with R=95 mm. from San Francisquito Bay, which is evidently identical with the sea-stars from the same place which are recorded in the first report as *Asterias forreri*. As Fisher's revision of the Pacific coast Asteriidae is not yet published, I let the name stand as in the former report, to prevent any possible confusion later on.

### **OPHIUROIDEA**

Since the publication of the first report, the classification of the ophiurans has undergone quite a revolution and the sequence of the species is almost reversed. To facilitate comparison and prevent confusion, it seems best to follow the sequence of species that was used in the earlier report. Fortunately, no changes of nomenclature are necessitated by the activity of recent years in ophiuran taxonomy.

### ***Ophiura leptoctenia* H. L. Clark**

*Ophiura leptoctenia* H. L. CLARK, 1911, Bull. U. S. Nat. Mus., No. 75, p. 51.

An additional specimen, 6 mm. across the disk, from Station 5694 calls for no comment.

### ***Ophiura superba* (Lütken and Mortensen)**

*Ophioglypha superba* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 116.

*Ophiura superba* MEISSNER, 1901, Bronn's 'Thierreich,' II, pt. 3, p. 925.

There are six additional specimens, 14 to 28 mm. across the disk, from Station 5694. In one fairly perfect specimen, 18 mm. across the disk, the arms are 90 mm. long.

### ***Ophiocten pacificum* Lütken and Mortensen**

*Ophiocten pacificum* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 131.

Two badly damaged specimens, one from Station 5689 and one from 5694, are scarcely worth recording.



**Ophiernus polyporus** Lütken and Mortensen

*Ophiernus polyporus* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 109.

An additional specimen, 13 mm. across the disk, from Station 5682 throws no light on the question of the validity of this species.

**Ophiomusium glabrum** Lütken and Mortensen

*Ophiomusium glabrum* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 132.

There are five additional specimens from Station 5689. They are about 30 mm. across the disk and the arms are about 165 mm. long.

**Ophiomusium jolliense** McClendon

*Ophiomusium jolliense* MCCLENDON, 1909, Univ. of California Publ., Zoöl., VI, No. 3, p. 36.

There is a typical example of this species, 7 mm. across the disk, in the present collection, but it was not represented in the material reported on previously.

Station 5682. Off Cape St. Lucas, Lower California, 491 fms. Bottom Temp. 40.8°.

One specimen.

**Ophiomusium lymani** Wyville Thomson

*Ophiomusium lymani* WYVILLE THOMSON, 1873, 'The Depths of the Sea,' p. 172.

One of the 18 additional specimens now at hand from Station 5689 is larger than any in the earlier collection, measuring 32 mm. across the disk, while the others are from 13 mm. up.

**Amphiura diomedæ** Lütken and Mortensen

*Amphiura diomedæ* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 151.

An additional, well-preserved specimen from Station 5694 has the disk 15 mm. across and the arms about 180 mm. long.

**Amphipholis squamata** (Delle Chiaje)

*Asterias squamata* DELLE CHIAJE, 1828, 'Mém. Anim. s. Vert.,' III, p. 74, Napoli.

*Amphipholis squamata* VERRILL, 1899, Trans. Connecticut Acad. Sci., X, p. 312.

A tiny brittle-star with disk about 2 mm. across is evidently an *Amphipholis* but shows no characters by which it can be distinguished from the ubiquitous species of Europe and eastern North America. Of course, were it full grown, it might show distinctive characters, but, as it



is, no other course seems right than to refer it to the cosmopolitan *squamata*. There was no representative of the genus in the earlier collection. The present specimen bears the label—"Middle of east side of Cerros Island, March 12, 1911." This island is off the western coast of Lower California.

***Ophiacantha normani* Lyman**

*Ophiacantha normani* LYMAN, 1879, Bull. Mus. Comp. Zoöl., VI, p. 58.

There are 51 additional specimens of this common brittle-star from Station 5694. They range from 9 to 17 mm. across the disk.

***Ophiacantha parasema*<sup>1</sup>, new species**

Disk about 22 mm. in diameter and 8 to 10 mm. thick; arms all broken near base, 4 to 5 mm. wide, the longest basal piece little more than 10 mm. long. Disk covered with a rather thick soft skin, the surface of which bears numerous crowded, more or less circular, minute plates, each of which carried a single, very acute, slightly rough spine. These spines are relatively thick at the base and taper to the sharp point; they are considerably longer than the diameter of the plate and hence the disk appears to be crowded with them. The longest are about a millimeter in length. Radial shields completely concealed and apparently wanting, but when the inner surface of the disk is examined, they can be detected as thin, flat plates, about 3 mm. long and half as wide, lying side by side, nearly parallel but scarcely in contact.

Upper arm plates quadrilateral, overlapping, with distal margin strongly convex and lateral margins converging proximally. The basal plate has a slightly convex proximal region and the lateral margins are a little concave. It is about as long as wide, but all the succeeding plates are much wider than long. There are, however, only half a dozen upper arm plates on the longest arm fragment present and it is hard to say how much of their shortness and overlapping is due to the highly contracted condition of the arms. For the three fragments that are still attached to the disk are pulled back dorsally so strongly that the upper surface rests against the disk, much as occurs in the usual specimens of *Ophiotholia*, and, when forcibly laid down horizontally, their upper surfaces are markedly concave from the evident contraction of dorsal muscles. Side arm plates moderately large, the spine-bearing ridges prominent, not meeting above, but apparently meeting narrowly below between the under arm-plates. It is possible however that in a relaxed arm, lying horizontally, the distal margin of the under arm-plates would overlies and conceal the side arm plates in the median line. Each side arm plate bears 6 or 7 arm-spines, of which the uppermost is probably the longest, or the next to the uppermost perhaps, and the lowest shortest; as all are broken, neither their actual nor relative lengths can be determined. They are glassy, acicular, longitudinally ridged and somewhat rough, but not thorny; the longest was evidently longer than the arm segment and apparently equalled two segments at least. Under arm plates small, depressed at center so that they are distinctly concave, quadrilateral, with rounded corners and concave lateral margins. They are not in contact in the present condition of the arms.

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<sup>1</sup>παράσημος = spurious, in reference to its not being a typical member of the genus.



Tentacles long and basally large, scarcely contracted at all. Tentacle pores large, guarded by three tentacle-scales which were apparently somewhat spiniform, but as all are broken at the tip their actual form is uncertain.

Interbrachial spaces below covered with thin, soft skin, with a few spine-bearing scales like those of the dorsal surface; these are most numerous, naturally, near the disk margin and are wanting near the mouth. Genital slits conspicuous, especially orally, margined by well-developed genital plates and at the oral end by the adoral plates and side arm plates. Oral shields conspicuous, nearly three times as wide as long, except the madreporite in which the length almost equals the width; the proximal margin has a distinct sharp median angle, but the narrow lateral angles are rounded. Adoral plates L-shaped, the tip of each branch expanded, especially the shorter; they meet broadly in front of oral shield, but abut on the first under arm plate at the other end. Oral plates rather large and a little swollen. Teeth in a vertical series of about 4, bluntly pointed, about twice as long as wide. Oral papillæ 4 on each side, the smallest ones distalmost, the largest at apex of jaw; the largest are as long as the teeth but not quite so wide. Besides the oral papillæ, the sides of the jaw are armed with conspicuous oral tentacle-scales; the first oral pore is guarded by two large ones, as big as the smaller oral papillæ but of course above them (apparently below, when the mouth-parts are being examined); the outer pore is guarded by three similar spiniform scales which are nearly at the same level and in line with the oral papillæ. Color pale gray.

TYPE.—Cat. No. —, U. S. Nat. Mus., from Station 5694.

Station 5694. Southwest of Santa Cruz Island, California, 640 fathoms.

One specimen.

The actual relationships of this brittle-star are dubious, owing to the defective condition of the specimen. The swollen disk and dorsally contracted arms, with the apparent absence of radial shields, remind one of *Ophiotholia*, but the mouth-parts are quite like many species of *Ophiacantha*. If the distal part of the arms were present, we should be better able to decide whether the relationship to *Ophiotholia* is at all close. Under existing conditions, it seems better to put the species in *Ophiacantha*, although it is obvious that it is not closely related to any species of that genus. The whole family of the Ophiacanthidæ needs revision with a careful comparison of internal skeletal plates which have hitherto been largely ignored. When this revision is made there will no doubt be a considerable increase in the number of genera which should be recognized.

### *Ophiocoma æthiops* Lütken

*Ophiocoma æthiops* LÜTKEN, 1859, 'Add. ad Hist.,' pt. 2, p. 145.

A very small brittle-star bearing every indication of being an *Ophiocoma*, and certainly not *O. alexandri*, is referred to this Panamic species. The disk is less than 2 mm. across, prettily variegated, as are



the arms, with yellow-brown and cream-color. Accompanying this specimen is a slip on which is written: "Lower California on oyster shells. No locality label." Only a single specimen of *æthiops* was in the original collection and that was from Angel de la Guardia Island in the Gulf of California.

***Ophiocoma alexandri* Lyman**

*Ophiocoma alexandri* LYMAN, 1860, Proc. Boston Soc. Nat. Hist., VII, p. 256.

A young specimen of this species, 4 mm. across the disk and yellow-brown in color, is very finely preserved, but, like the young *æthiops*, it is accompanied by a slip reading "Lower California. No locality label. On oyster shells."

***Ophiothrix spiculata* Le Conte**

*Ophiothrix spiculata* LE CONTE, 1851, Proc. Acad. Nat. Sci. Philadelphia, V, p. 318.

There are 30 very badly preserved small specimens of this common Panamic brittle-star with the disk 2 to 7 mm. across. They bear a label "D 5695" but this locality is obviously wrong, as the depth at Station 5695 was 534 fms. and *spiculata* is essentially a littoral species. It has been recorded from depths near the 100 fms. line, but that is extreme. The label with the specimens bears the date April 26, 1911 and the specimens themselves indicate that they were taken in very shallow water.

***Astroschema sublæve* Lütken and Mortensen**

*Astroschema sublæve* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 187.

There are two more specimens from Station 5695, one an adult with disk 13 mm. across and arms fully 200 mm. long, but only 3 mm. in diameter; the other very young, with disk smooth, only 2 mm. across and arms so tightly coiled on the gorgonian, on which both it and the adult are borne, that they cannot be measured.

***Asteronyx excavata* Lütken and Mortensen**

*Asteronyx excavata* LÜTKEN AND MORTENSEN, 1899, Mem. Mus. Comp. Zoöl., XXIII, p. 185.

There is a single additional specimen, 22 mm. across the disk, on a gorgonian from Station 5688.

**ECHINOIDEA**

***Eucidaris thouarsii* (Agassiz and Desor)**

*Cidaris thouarsii* AGASSIZ AND DESOR, 1846, Ann. Sci. Nat., VI, p. 326.

*Eucidaris thouarsii* DÖDERLEIN, 1887, 'Jap. Seeigel,' p. 42.



There are some good representatives of this species in the present collection and they show no little diversity in form. For example, one 42 mm. in diameter is 24 mm. high, v.d. thus equal to less than .60 h.d., while another specimen 58 mm. in diameter is 41 mm. high, v.d. equaling more than .70 h.d. In the best-preserved specimens the spines are nearly or quite equal to the diameter of the test. In one specimen there are 7 or 8 coronal plates in a series, while in another there are 9 or 10, a very large number for *thouarsii*. The specimens from Espiritu Santo bear a label reading "Enemies of pearl oyster at propagating plant." It seems highly improbable that this can be a fact, though it may be the impression of the pearl-shell growers. It would be interesting to know in just what way the sea-urchin is supposed to injure the pearl shells.

Espiritu Santo.

San Francisquito Bay, east coast of Lower California.

Six specimens.

#### **Centrostephanus coronatus** (Verrill)

*Echinodiadema coronata* VERRILL, 1867, Trans. Connecticut Acad., I, p. 294.

*Centrostephanus coronatus* A. AGASSIZ, 1872, Illust. Cat. Mus. Comp. Zoöl., VII, p. 97.

There are five unusually large specimens at hand, 45 to 50 mm. h.d.: thus twice as big as the largest in the earlier collection. The coloration too indicates maturity, for the banded spines of the young are no longer in evidence. Although all of the primaries have the tips broken off, they are long enough to show the absence of bands; they are deep claret distally but browner basally.

San Francisquito Bay, east coast of Lower California.

#### **Astropyga pulvinata** (Lamarck)

*Cidarites pulvinata* LAMARCK, 1816, 'Anim. s. Vert.,' III, p. 59.

*Astropyga pulvinata* AGASSIZ AND DESOR, 1846, Ann. Sci. Nat., VI, p. 345.

This interesting sea-urchin was not represented in the former collection, but there is a fine series at hand now, ranging from 15 to 95 mm. in diameter. Unfortunately, they are not in the best of condition, the small ones in particular being more or less damaged. On the larger specimens the spines are mostly missing or broken. The most interesting feature of these *Astropygas* is the coloration. All specimens of *pulvinata* which I have seen hitherto have had a dull greenish ground color, in marked contrast to the deep red of *A. radiata*. The present specimens however show that the ground color in *pulvinata* is deep, purplish red at and above the ambitus and that the greenish color of dry museum mate-



rial is due to the peeling off and loss of the red epidermis, which appears to flake off and disappear very easily. A very constant feature of the coloration of *pulvinata*, conspicuous in all but one of the present series, is a yellowish triangular spot in each interradius just above the ambitus. This is usually visible even in the greenish specimens and is very noticeable in the red ones. Apparently this spot is pale yellow, or possibly even white, in life.

San Francisquito Bay, east coast of Lower California.

Fifteen specimens.

#### ***Arbacia incisa* (A. Agassiz)**

*Echinocidaris incisa* A. AGASSIZ, 1863, Bull. Mus. Comp. Zoöl., I, p. 20.

*Arbacia incisa* H. L. CLARK, 1913, Bull. American Mus. Nat. Hist., XXXII, p. 220.

There is a fine series of this species in the present collection, for the most part in good condition. They range from 10 to 38 mm. in diameter. The relative length of the primary spines shows some diversity; in the individual with the test 38 mm. h.d., the spines are 39 mm. long, but in one having h.d. 16 mm. the spines are 23 mm. long. Half a dozen of the specimens lack a locality label but the others are from San Francisquito Bay, east coast of Lower California.

Twenty specimens.

#### ***Clypeaster speciosus* Verrill**

*Clypeaster speciosus* VERRILL, 1870, American Journ. Sci., (2) XLIX, p. 95.

This fine clypeastroid was not represented in the first collection, but beautifully preserved specimens are now at hand, 76 mm. long, 66 mm. wide and 18 mm. high. They have the lower side very flat and the color is a deep, dull purple.

San Esteban Island, Gulf of California.

Two specimens.

#### ***Encope californica* Verrill**

*Encope californica* VERRILL, 1871, Trans. Connecticut Acad. Sci., I, p. 586.

This remarkable clypeastroid was also wanting in the earlier collection, although two other species of *Encope* were represented. The three species are easily distinguished from each other and show no tendency to intergrade or hybridize. It is possible that they do not occur together at any given place, but that each species has its own particular habitat. The 'Albatross' collections indicate that *californica* and *grandis* occur at the same locality and that *grandis* and *micropora* are



both found at Tiburon Island, but that of course does not prove that they are actually living together at the same spot.

The specimens of *californica* in the present lot show interesting diversity in the proportions of length and breadth. A typical specimen is 93 mm. long and 93 mm. wide, but three others are 95 by 93, 104 by 101 and 116 by 110. As a rule, the length is slightly greater than the width, but occasionally the width is greater; thus one specimen 109 mm. long is 112 mm. wide. The color of the dry specimens is brown, with a marked violet tinge around the lunules and along the margin.

Conception Bay, east coast of Lower California.

Twenty-one specimens.

#### **Encope grandis** Agassiz

*Encope grandis* AGASSIZ, 1841, 'Monogr. Echin., Scutelles,' II, p. 75.

There are additional specimens of this extraordinary creature at hand from new localities. The length exceeds the width, the measurements being 98 by 93 mm. and 100 by 98.

Conception Bay, east coast of Lower California.

San Francisquito Bay, east coast of Lower California.

Two specimens.

#### **Urechinus loveni** (A. Agassiz)

*Cystechinus loveni* A. AGASSIZ, 1898, Bull. Mus. Comp. Zoöl., XXXII, p. 79.

*Urechinus loveni* MORTENSEN, 1907, 'Dan. Ingolf.-Exp., IV, Echinoidea,' pt. 2, p. 50.

There are two additional specimens of this odd and fragile sea-urchin from Station 5684. One is 78 mm. long, 57 mm. wide and 35 mm. high, while the other is 75 by 44 mm.

#### **Schizaster townsendi** A. Agassiz

*Schizaster townsendi* A. AGASSIZ, 1898, Bull. Mus. Comp. Zoöl., XXXII, p. 82.

Additional material from Station 5697 consists of eight more or less complete specimens, 40 to 50 mm. long, and fragments of others.

#### **Brissopsis pacifica** (A. Agassiz)

*Toxobrissus pacificus* A. AGASSIZ, 1898, Bull. Mus. Comp. Zoöl., XXXII, p. 83.

*Brissopsis (Toxobrissus) pacifica* MORTENSEN, 1907, 'Dan. Ingolf.-Exp., IV, Echinoidea,' pt. 2, p. 44.

There are 42 additional specimens, 10 to 30 mm. long, and many fragments, from Station 5675.



**HOLOTHURIOIDEA*****Molpadia musculus* Risso**

*Molpadia musculus* RISSO, 1826, 'Hist. Nat. Princip. Product. Europe Mer.,' p. 293.

There is a single *Molpadia* from Station 5684, in fine condition, 80 mm. long by 25 mm. in diameter where largest, and with the caudal portion 13 mm. long. The color is pale gray and there are no phosphatic bodies. The calcareous particles seem to warrant referring it to this species, but it is certainly not a typical example.

***Cucumaria abyssorum* Théel**

*Cucumaria abyssorum* THÉEL, 1886, 'Rep. Voy. 'Challenger,' Zool.,' XXXIX, p. 66.

There are two additional specimens from Station 5684 and five from 5691. They are well preserved and several show their ten tentacles. They are 50 to 95 mm. long and in the largest the genital papilla is conspicuous.

***Psolus squamatus* (O. F. Müller)**

*Holothuria squamata* O. F. MÜLLER, 1776, Proc. Zool. Dan., p. 232.

*Psolus squamatus* MCANDREW AND BARRETT, 1857, Ann. Mag. Nat. Hist., (2) XX, p. 45.

There is another large *Psolus* at hand from Station 5695, measuring 80 mm. long by 55 mm. wide and 30 mm. high. It seems to me almost incredible that these specimens can really have been taken at a depth of 534 fms. and not show any differences to distinguish them from specimens taken in shallow water on the Norwegian coast. The species of *Psolus* are in need of critical revision and the Pacific coast material is not at present sufficient to make such a revision satisfactory.

***Thyonepsolus nutriens* H. L. Clark**

*Thyonepsolus nutriens* H. L. CLARK, 1901, Zool. Anz., XXIV, p. 168.

There is a small psolid at hand with only the unsatisfactory label "Gulf of California" to indicate whence it came. It is 12 mm. long by 6.5 mm. wide and about 4 mm. high. The calcareous deposits in the sole can be roughly grouped in three classes and are almost exactly like those of *Psolidium dorsipes* Ludwig. But the dorsal surface is quite unlike *Psolidium* and is exactly as described for *Thyonepsolus*, soft, thick, with no visible scales or plates, and very numerous pedicels not arranged in longitudinal series. The validity of *Thyonepsolus* has been questioned and some have relegated the genus to the synonymy of *Psolidium*, but



the examination of the present specimen confirms my belief that it is a recognizable, natural group. In one respect, however, this specimen from the Gulf of California is unlike those from Monterey, California, and that is in the deposits of the sole. It is probable, however, that my original description failed to recognize the diversity to be found in these desposits.

***Benthodytes sanguinolenta* Théel**

*Benthodytes sanguinolenta* THÉEL, 1882, 'Rep. Voy. 'Challenger,' Zool.,' XIII, p. 104.

There are three fairly well preserved specimens of this deep sea holothurian, 125 to 175 mm. long, but they have with them no locality label. The 'Albatross' met with the species at four stations in depths exceeding one thousand fathoms.

***Pseudostichopus mollis* Théel**

*Pseudostichopus mollis* THÉEL, 1886, 'Rep. Voy. 'Challenger,' Zool.,' XXXIX, p. 169.

There are three additional specimens from Station 5695. They are smooth, shiny white, and 110 to 150 mm. long.

***Stichopus parvimensis* H. L. Clark**

*Stichopus parvimensis* H. L. CLARK, 1913, Bull. American Mus. Nat. Hist., XXXII, p. 234.

A young *Stichopus* only 40 mm. long seems to belong to this species. The dorsal papillæ have very dark tips.

Point San Bartolomé, west coast of Lower California. "Boat dredge."

***Holothuria lubrica* Selenka**

*Holothuria lubrica* SELENKA, 1867, Zeitschr. f. w. Zool., XVII, p. 329.

The specimens listed in the earlier report bore no locality label, but of those now at hand only two lack such a label. The specimens run from 20 to 160 mm. in length, the last being a maximum for the species. It is interesting to note that the species occurs on both sides of Lower California as well as far up in the Gulf.

Angel de la Guardia Island, Gulf of California.

Pichilingue Bay, east coast of Lower California.

Santa Maria Bay, west coast of Lower California.

Eight specimens.



**Holothuria monacaria** (Lesson)

*Holothuria* (*Psolus* Oken) *monacaria* LESSON, 1830, 'Cent. Zool.,' p. 225.

*Holothuria monacaria* JAEGER, 1833, 'De Holoth.,' p. 24.

A small holothurian, 60 mm. long from Pichilingue Bay, east coast of Lower California, seems to represent this Indo-Pacific species, although it has not previously been recorded from the coast of America. A much smaller specimen, 15 mm. long, with no locality label other than "Lower California," is too young for certain identification, but may, for want of a better place, be referred to this species. I have little doubt however, that when the genus *Holothuria* is critically and carefully revised, the range of true *monacaria* will not include the western coast of America.







Article VII.—STUDIES ON NORTH AMERICAN BLOOD FLUKES<sup>1</sup>

BY HORACE W. STUNKARD

PLATES II TO XIII

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## INTRODUCTION

The group of blood-infesting trematodes as at present constituted comprises three families, the Schistosomidæ, the Spirorchidæ and the Aporocotylidæ. The first of these families is the best known and con-

<sup>1</sup>Contribution from the Biological Laboratory, New York University, and the Department of Lower Invertebrates, The American Musum of Natural History.



tains the diecious forms parasitic in the vascular system of birds, cattle, and man. The Spirorchidæ and Aporocotylidæ are hermaphroditic forms, the former occurring in the blood vessels of turtles and the latter in those of fishes. Certain morphological characters are common throughout the group of blood flukes, but within the families and even within some of the genera great morphological disparities are present. The fish parasites are without organs of adhesion; one group of turtle parasites has only an oral sucker, while the other has both oral sucker and acetabulum; and in the family Schistosomidæ there are genera without suckers and others with both oral and ventral adhesive organs. In the Aporocotylidæ the genital pore is dorsal; in the Spirorchidæ it is either dorsal or ventral and somewhat lateral; and in the Schistosomidæ it is ventral, either in the median line or at the right or left of it. Among the blood flukes there are genera with a long coiled uterus containing many eggs and others with a short uterine portion of the female genital duct containing a single egg. These major points of distinction are associated with minor differences and constitute a large and unusual list of anomalies in the group of blood-infesting trematodes. Probably no other trematode group manifests such unusual morphological diversity and no satisfactory explanation has as yet been offered for the presence of the structural dissimilarity that exists in the group of blood-inhabiting trematodes. The discovery of new blood flukes in North America and a study of their distinctive features will, I believe, afford evidence of considerable value in the interpretation of data accumulated in the study of the previously known forms. The addition of such information should aid materially in an understanding of the morphological and biological characters of other blood flukes.

For the sake of completeness and also to facilitate comparison of previously described forms with new ones described in this paper, a brief outline and description of the families and their genera is given.

#### **SCHISTOSOMIDÆ** Looss, 1899

Elongate forms parasitic in the vascular system of birds and mammals; sexes separate; pharynx absent; intestinal ceca unite to form a single intestine. Suckers present or absent; acetabulum when present anterior to genital pore. Male with four or more testes; may be widened posterior to acetabulum and have sides curved ventrally to form a gynecophoric canal. Female more slender than male; ovary elongate; vitellaria extensive, extend far posteriad.

The family Schistosomidæ as characterized by Odhner 1912 contains the genera *Schistosoma*, *Bilharziella*, *Gigantobilharzia*, *Ornithobilharzia*, and *Austrobilharzia*<sup>1</sup>.

<sup>1</sup>While this paper was in press, Tanabe, in the Journal of Parasitology, June 1923, IX, pp. 183-199, described the structure and life history of a new schistosome, *Schistosomatium pathlopticum*.



**SCHISTOSOMA** Wienland, 1858

SYNONYMS.—*Gynæcophorus* Diesing, 1858; *Bilharzia* Cobbold, 1859; *Thecosoma* Moquin-Tandon, 1860.

Schistosomidæ with long filiform females and shorter males. Male with gynecophoric canal in which the female is enclosed. No cirrus sac; no Laurer's canal; eggs with spines and no lids. Miricidia ciliated, with large glandular cells discharging anteriorly beside the gastric sac. Development in various snails. Cercariæ with forked tails and no eye spots; develop in sporocysts; enter mammalian hosts through skin or mucosa and pass into blood vessels.

The type species, *S. hæmatobium*, was discovered in 1851 by Bilharz in Cairo, Egypt. Its structure has been known since the classical description of Looss (1895). In 1915, Leiper discovered its life cycle, the miricidia entering snails of the genus *Bullinus*. The sporocysts give rise to daughter sporocysts and these to cercariæ. Adults live in the pelvic veins. The eggs have a terminal spine and are voided in the urine.

Two other species, *S. japonicum* Katsurada, 1904, and *S. mansoni* Sambon, 1907, occur in man, and several species have been reported from various species of cattle.

The splendid account of this genus by Castellani and Chalmers (1919), dealing with the literature, classification, anatomy, life history and pathology of the human schistosomes, renders further summary here unnecessary.

**BILHARZIELLA** Looss, 1899

Female shorter than male, both much flattened; integument spined; intestine unpaired; genital pore lateral, usually on the left side. Cirrus sac present, well developed, seminal vesicle largely outside of cirrus sac. Prostate large, longer than the cirrus. Female less elongated than in other schistosomes; ovary short, weakly spiral; vitellaria less than one-half length of body; uterus short, contains only a single egg.

Type species: *B. polonica*.

Genus proposed by Looss to include *B. polonica* Kowalewski, 1895, and *B. kowalewski* Parona, 1896, parasites in the vascular system of various species of birds. Braun (1902) added *B. pulverulenta*, a form in which suckers are entirely lacking, and transferred *Distomum canaliculatum* Rudolphi to this genus.

**GIGANTOBILHARZIA** Odhner, 1910

Sexes separate but worms not paired as in *Schistosoma*; no suckers or spines; esophagus as in other schistosomes; excretory pore at posterior end; short bladder, which divides almost immediately; vitellaria extend to posterior end of body; single egg in uterus. Parasitic in *Larus fuscus*.

Single species: *G. acotylea*.



**ORNITHOBILHARZIA** Odhner, 1912

Female shorter than male; suckers present with small spines. Male with gynecophoric canal; copulatory apparatus small, on posterior wall of acetabulum. Seminal vesicle entirely outside a rudimentary cirrus sac; no prostate; genital pore slightly left. Female long, threadlike, flattened; ovary long, strongly spiral; vitellaria extend over two-thirds of body length; single egg present in uterus.

Type species: *O. intermedia* Odhner, 1912.

Odhner (1912) removed the species *Bilharziella canaliculata* and *B. kowalewski* to this genus.

**AUSTROBILHARZIA** Johnston, 1917

Male shorter than female; gynecophoric canal present; cirrus sac well developed, encloses vesicula seminalis; prostate present; two suckers, without spines. Female has anterior filiform and posterior flattened regions; acetabulum stalked as in the male, oral sucker absent; ovary, long, spiral; vitellaria in posterior third of body; single egg present in uterus. Parasitic in *Larus novæ hollandiæ*.

Single species: *A. terrigalensis*.

**APOROCOTYLIDÆ** Odhner, 1912

Hermaphroditic blood flukes, parasitic in the heart and arterial system of various species of fishes. Suckers absent; only adhesive structures are cuticular spines. Pharynx absent; esophagus long; ceca H-shaped; two anterior and two posterior crura; excretory pore terminal, slightly dorsal; unpaired excretory bladder with two long vesicles which extend forward below the ceca; genital pore dorsal near posterior end of body, median or lateral; testes numerous, anterior to ovary; cirrus small; vitellaria well developed, duct single.

The family Aporocotylidæ was proposed by Odhner to contain the genera *Aporocotyle* and *Sanguinicola*. In the original description Odhner (1900) reported *Aporocotyle* as an ectoparasite from the gills of the flounder. Plehn (1905) described *Sanguinicola* as a turbellarian and three years later (1908) decided it was a monozoic cestode. Odhner reinvestigated these forms and discovered their true nature. In his paper (1911) announcing them as blood parasites, he discussed the fundamental agreement between their structure and that of *Deontacylix ovalis*. The latter form had been described by Linton (1910) from the intestine of *Kyphosus sectatrix*, and, unable to recognize any near resemblance between it and any then known group, he proposed a new suborder to contain it. It is an interesting and noteworthy fact that in the original descriptions the true character of not one of these forms was recognized and only *Sanguinicola* was originally reported from the blood vessels.

Communicating with Dr. Linton, I learned that his material of *Deontacylix* consisted of specimens mounted *in toto* on two slides. One



of these was sent to Dr. Odhner in December 1911 and, failing to reach its destination, the other was sent in March 1912. The latter slide with all the available material of the species was kindly loaned to me for examination. It is difficult to identify and trace structures with certainty in the mounted specimens and I am unable to add anything to Linton's description of the form. His figure is an accurate representation of the specimen and his description as complete as possible from the material at hand. In the letter accompanying the slide he expresses the belief that the form is a blood parasite. I think there is a strong probability that the specimens came originally from the mesenteric blood vessels and on the basis of morphological similarity I assign the form to the family Aporocotylidæ.

In a postscript to his article announcing *Sanguinicola* as a blood fluke, Odhner (1911) reported experiments and published a series of drawings done by Looss on the life history of this form. Because of morphological similarity, Odhner had suspected that *Cercaria cristata*, a forked tailed cercaria present in several species of European snails, was the larval stage of *Sanguinicola*. The work of Looss confirmed and established this suspicion. Looss demonstrated that this cercaria develops into *Sanguinicola* in goldfish and carp. Infected snails were placed in aquaria with these fishes and heavy infection followed, resulting in the death of the fish. All stages in the transformation of the cercariæ to the adult worms in the heart were obtained.

#### **SPIRORCHIDÆ** Stunkard, 1921

Slender, blood-inhabiting trematodes with slightly developed musculature and one or two weak suckers. Pharynx absent. Testes lobed, multiple, anterior and sometimes also posterior to the ovarian complex.\* Ovary lobed; Laurer's canal present; uterus short. Eggs large, thick shelled, discharged singly.

The name Spirorchidæ was proposed by the writer (1921) for the family outlined by Ward (1921) to contain the blood flukes of turtles when the name Proparorchidæ Ward became invalidated through the synonymy of the genera *Spirorchis* and *Proparorchis*. As originally erected, the family contained only the genera *Spirorchis* and *Hapalotrema*. Because of unique differences these genera were referred to separate subfamilies, Spirorchinæ and Hapalotremiæ. The following year the discovery of two new genera, one of which belongs to each of the subfamilies, made it possible for the writer (1922) to characterize these groups with more definiteness. The discovery of another new genus, which is described in the present paper, further confirms the arrangement.



**Spirorchinæ** Stunkard, 1921

Hermaphroditic, blood-inhabiting monostomes with weak oral sucker. Esophagus without pharynx and surrounded by secretive cells which are more numerous near its posterior end. Ceca end blindly near posterior end of body; excretory vesicle small, dividing almost immediately into lateral collecting ducts. Testes numerous, arranged in a linear series in the intercecal area anterior to the ovary; cirrus sac small; ovary dextral in position between the testes and the genital pore; seminal receptacle and Laurer's canal present; vitellaria both extra and intercecal; genital pore ventral, sinistral, near the posterior end of the body; uterus short, containing a single oval egg.

The type genus, *Spirorchis*, was described by MacCallum (1918) but this author unfortunately omitted the specific name intended for the species. MacCallum reported the form from the intestine of *Clemmys insculpta*. This paper appeared while I was in the U. S. army in France. On my return to New York University after release from military service, I noticed the description of the form and was struck by the likeness of the parasite described by MacCallum to certain trematodes I had collected from the vascular system of several species of turtles during the years 1913 to 1916, while a graduate student in the department of zoölogy of the University of Illinois. The blood flukes I had collected and the form described by MacCallum are monostomes of similar size and shape; they agree in position and character of oral sucker, position and extent of intestinal ceca, position and extent of vitellaria, vitelline ducts and receptacle, position and shape of ovary, oviduct and uterus, position and extent of testes, shape and location of seminal vesicle and vas deferens, as well as position of the excretory pore. They are alike in the character of intestinal content, which led MacCallum to describe the form as a hæmatophagic trematode. The only points of difference are to be found in the statement of MacCallum that in *Spirorchis* a pharynx is present and that the genital pore is median near the posterior end of the body, while in my material a pharynx is absent and the genital pore is lateral, slightly posterior to the level of the ovary. Conferring with Dr. MacCallum, I learned that the description was made from specimens mounted *in toto*, but unfortunately at that time his slide could not be found. Dr. MacCallum examined several of my specimens and noted the similarity between them and the form he had described, but was not certain whether they were the same.

Ward (1921) described a new trematode from the heart and arteries of various species of North American fresh-water turtles, giving to the parasite the name *Proparorchis artericola*. In the introduction of his paper he stated that the parasite had been under observation in the zoölogical laboratory of the University of Illinois for several years, and added:



Since the material is easily obtained, it will afford perhaps the best opportunity available in this country for the laboratory study of forms adapted to this particular environment, so that, despite the incompleteness of the observations, the publication of this note is justified. It is further called for by the fact that several others, who had their attention called to this species, plan to give it more detailed study than I can make at the present time, and will be glad to have a record of the facts thus far determined in order to utilize them as a basis for further study.

He described the blood flukes of North American turtles as belonging to a single species, and says: "according to records of collection here, it has been met with in *Pseudemys elegans* from Havana, Illinois, in *Malacoclemmys leseurii* in Newton, Texas, in *Pseudemys scripta* from Raleigh, N. C., and in *Chrysemys marginata* from Fairport, Iowa."

Although he described *Proparorchis artericola* as the type and only species present in fresh-water turtles, he says:

The data in my possession are not all referable to the single species which has just been described. In details of structure, in the location in the host in which they have been observed, and in some other details, certain specimens differ so distinctly from the account above that I can not at present include them under the same heading. It is possible that they represent phases in the life cycle of a single species. I am inclined to think the structure of this worm too delicate for one to consider it probable that any part of its life history could be passed in the intestine. But such a transfer must still be kept in mind as a possibility. In my opinion it is much more likely that further study will disclose the presence of several species parasitic in the blood of reptiles and amphibia.

Discussing the form described by MacCallum, Ward pointed out that "MacCallum's description is brief and in some details confused, since the dimensions given are clearly wrong and the text does not agree in full with the illustration." Comparing the structures described in MacCallum's text and shown in the figure accompanying it with the form he had described, Ward was "impressed by the general likeness," and regarded the form as "undoubtedly closely related" to the blood flukes. However, the differences were too great to warrant a final conclusion, and Ward accepted MacCallum's diagnosis, assigned to the worm the specific name *innominata*, and included the genera *Spirorchis* and *Proparorchis* in a new subfamily, Proparorchinae. He removed the genus *Hapalotrema* Looss from the subfamily Liolopinae Odhner, and included it with the Proparorchinae in a new family, Proparorchidae.

Publication of the results of my studies had been delayed because of uncertainty regarding the relation of the blood flukes to the genus *Spirorchis*, and also because of difficulty in specific determination of the material at hand. Both of these problems were recognized and discussed by Ward, although his work did little toward an adequate or final disposition of them. Shortly after the appearance of Ward's paper, Mac-



Callum found and sent me the type specimens of *Spirorchis*. Examination of this material afforded a ready solution for the first of the problems involved. The structure described as a pharynx in *Spirorchis* is in reality the esophageal commissure, and no pharynx is present. The genital pore is ventral, below the cecum of the left side, a short distance posterior to the level of the ovary. Consequently, I published (1921) a further description of the form and corrected the original statements regarding the presence of a pharynx and the location of the genital pore. In this paper also I gave a record of my dissections, pointed out that I had first collected blood flukes from turtles in 1913 while a graduate student at the University of Illinois, and that the distribution and list of hosts as given by Ward agree almost exactly with my records of collection while at the University of Illinois. There can be no question that the specimens I had collected are the same as those described by Ward. On the basis of morphological similarity and the strong suspicion that the specimens of *Spirorchis* came originally from the vascular system, I announced the identity of *Spirorchis* and *Proparorchis*. With the disappearance of the generic name *Proparorchis*, the subfamily and family names Proparorchinae and Proparorchidae also disappear. At that time *Spirorchis* was the only known genus of the subfamily to which it belongs and I designated it as type, proposing the subfamily name Spirorchinae. For the family outlined by Ward under the invalidated name Proparorchidae, I proposed the name Spirorchidae, and designated *Hapalotrema* as type of a new subfamily Hapalotremine in the family Spirorchidae.

In a paper dated August, 1921, MacCallum accepted the names Spirorchinae and Spirorchidae but objected to the name *innominata* proposed by Ward for the species described by him from the intestine of *Clemmys insculpta*, and for which the name originally intended was omitted in the published account. He says, "Unfortunately, through an error the specific name *eustreptos*, which was intended, was omitted. Ward in his paper of March 1921 (*Journal of Parasitology*), without consulting me, and without studying the form, suggests the specific name *innominata*. But the name is not acceptable and I maintain the name *Spirorchis eustreptos*." The disagreement between these two investigators is regrettable, but since *innominata* was the first specific name to be published after the generic name *Spirorchis*, the rules of priority sustain its validity.

Referring to the species described by him as *Spirorchis* (specific name omitted), MacCallum reported that he had found the same worm in 1912 in the lung of *Chrysemys picta*. He reported also the discovery in



the lung of *Emys blandingii* of a single specimen which he stated evidently belongs to that genus. In his description of the worm there is the following significant statement: "It is quite possible that this worm may have been lying in the blood vessels of the lung, since Ward has clearly shown that his entirely similar *Proparorchis* is to be found in the blood stream." Later in the paper, discussing the question of a pharynx in the genus, he says: "In the case of *Spirorchis eustreptos* I am now satisfied that the worm should not be credited with a pharynx although in one of the three specimens the outline of a pharynx may be distinctly seen in the position given it in the plate by the artist. None of THESE BLOOD FLUKES apparently are possessed of the usual pharynx." The discovery of *Spirorchis innominata* in the lung would signify that it is not normally a parasite of the intestine and the later statement of MacCallum indicates that he now regards it as a blood fluke. This recognition of the vascular system as the normal habitat of the form and the further agreement that a pharynx is absent confirm the position taken by me in declaring the synonymy of *Spirorchis* and *Proparorchis*.

MacCallum considered the specimen found in the lung of *Emys blandingii* as a new species and for it he proposed the name *Spirorchis emydis*. The description in many respects is indefinite and incomplete, especially as regards the reproductive organs. The testes and seminal receptacle of the specimen are crushed, and neither the cirrus, metratrem, Laurer's canal or genital pore were observed. No definite specific characters are given, nor any evidence to sustain the specific identity of the form. It is impossible to recognize the species from either the description or the figure, and consequently, I believe, to recognize the validity of the specific name. I see no good reason for not regarding it as a synonym of *Spirorchis innominata*.

The following year (1922) I announced the discovery of two new genera of North American blood flukes, *Henotosoma* belonging to the subfamily Spirorchinae, and *Hapalorhynchus* belonging to the subfamily Hapalotremineae. A single species of each of these genera was described, *Henotosoma hæmatobium* and *Hapalorhynchus gracilis*.

For several years I have made a wide and careful search for blood flukes of North American turtles and have carried on experimental work, so far unsuccessfully, in an attempt to trace the complete life cycle of these forms. I have found these parasites in many different species of turtles ranging in distribution over the entire eastern half of the United States. Blood fluke infections have been observed in *Chrysemys marginata* from Iowa, Illinois, Indiana and Ohio; *Chrysemys picta* from



North Carolina, New Jersey and New York; *Clemmys guttata* (syn. *Chelopus guttatus*), *Terrapene carolina* (syn. *Cistudo carolina*), and *Chelydra serpentina* from the middle Atlantic states; *Pseudemys scripta* from Raleigh, North Carolina; and *Pseudemys elegans*, *Graptemys geographica* (syn. *Malacoclemmys geographicus*) and *Graptemys pseudo-geographica* (syn. *Malacoclemmys leseurii*) from the Mississippi valley. In not all of these species were adult forms of the parasite secured, but the characteristic appearance of the tissue filled with eggs of the parasite gives positive proof of infection. Since the eggs are deposited in the blood vessels and must work their way through the tissues to be voided with the fecal and urinary wastes of the host, a procedure which involves a very considerable extent of time, it is possible to find eggs in the tissues and feces long after the adults have disappeared from the vessels.

The present paper contains the results of these researches to date. Additions are made to the descriptions of *Henotosoma hæmatobium* and *Hapalorhynchus gracilis*, and a new genus, *Hæmatotrema* belonging to the subfamily *Spirorchinæ* is described. A study of the original specimens of *Spirorchis innominata* has made possible a more complete description of that form and five species in that genus are described. The types and figured specimens of the species here described as new are in the collection of The American Museum of Natural History.

#### SPIRORCHIS

This genus contains several species and produces a widely distributed and prevalent infection in many species of North American freshwater turtles. Adults live in the heart and arteries and have been found with greatest frequency in the heart, the pulmonary, carotid, and mesenteric arteries. The infection is often very heavy and as many as 90 per cent of the turtles from certain districts are parasitized. In one group of fourteen *Chrysemys picta* collected in the fall of 1920 from a single pond near Cold Spring on the Hudson, New York, every turtle harbored the parasite. Usually the number of worms obtained from a given host is not large, sixteen specimens from a painted turtle, *C. picta*, constituting the heaviest single infection found. Often only one or two specimens have been recovered, although there is always the possibility that some have been overlooked. Usually there are from four to eight flukes in each infected turtle.

The length of life of the worm after it enters the blood stream is unknown, but it must extend over a considerable period of time. Living specimens have been removed from the arteries of turtles kept over a



year in the laboratory. During this time there had been no opportunity for subsequent infection or reinfection and the parasites must have been acquired previous to the capture of the hosts.

The eggs are deposited in the blood vessels and distributed throughout the body of the host, especially in the tissue of the visceral organs. The eggs rupture the capillaries and pass into the tissue in enormous numbers, and the presence of eggs in the tissue is the first and best means of recognizing the infection. The eggs then work their way through the tissues of the host and are voided with the fecal and excretory material. All the tissues of the host become involved if the infection is heavy or of long standing. Eggs have been observed in the cerebral lobes of the brain and abound in the lungs, liver, spleen, kidneys, mesenteries and wall of the intestine. In the mesenteries and omenta and on the surface of the intestine and kidneys the arteries frequently appear as dark lines, due to the presence of tremendous numbers of eggs in these vessels. In the wall of the intestine the eggs are most prevalent between the peritoneal investment and the circular muscles and in the submucosa.

The worm is very fragile and delicate. Its presence in the smaller arteries can usually be detected by the dark lines of the intestinal ceca which are visible through the wall of the vessel, although in the larger arteries the wall is too thick to observe the parasite and it can be found only by dissection. These flukes are usually inactive in the arteries and it often requires extreme care to remove a specimen from the vessel without injuring it. In other cases, however, when freed in normal salt solution, the parasite manifests the most violent muscular reactions, exertions entirely unexpected from its delicate structure. These may involve the entire musculature, the contractions and elongations of the body alternating with such rapidity and force that it is almost impossible to follow them, or the lateral edges of the body may show a rapid undulatory movement. After a short time movement ceases and in many, if not in most, cases the parasite displays no motility at all. Sometimes the worm bends very slowly in the form of a loop, bringing anterior and posterior ends together. They straighten out on shaking and contract only slightly on the application of killing and fixing fluids.

Members of this genus are hermaphroditic monostomes, elongated and flattened in form. They are widest near the middle of the body and taper toward either end. Frequently the posterior end is slightly wider and less pointed than the anterior. The body is thin, especially at the edges, and very transparent. These forms are small. The largest observed, a specimen of *S. innominata*, measures 4 mm. in length and



0.66 mm. in width; the smallest, a specimen of *S. scripta*, is 1.18 mm. in length and 0.24 mm. in width. The length relative to width varies considerably in living specimens due to the contraction or elongation of the specimen.

The body is covered by a very thin cuticula without hooks or spines. The cuticula is easily shed or disintegrated, and a sticky substance is given off which tends to collect and hold bits of débris. The cuticular covering of the body is inturned at the oral sucker and forms the lining of the esophagus. In this region it is very thin, and the gland cells which encircle the esophagus open through it into the lumen of the canal. It is also reflexed at the genital and excretory pores, forming the lining of these ducts for a short distance.

The musculature of the body is very slight and consists of the dermo-muscular sac enclosing the entire worm, the muscles of the sucker, and weak muscular fibers in the walls of the ceca and the genital and excretory ducts. The body wall contains circular, longitudinal, and oblique fibers, but they are not separated into discrete layers; rather there is a reticulum of intermingled fibers. In sections it is possible to determine the relation of the fibers with considerable definiteness, and the circular fibers are external, with the longitudinal fibers between the outer circular and inner oblique fibrils. A loose network of branching and anastomosing parenchymatous fibers fills the body and extends across it, chiefly in a dorso-ventral direction. The muscles of the oral sucker consist of branched fibers, which pass from the external limiting membrane to the lining of the passage. The nuclei of this region are grouped concentrically near the limiting membrane (Fig. 13).

The digestive system is of the triclad type, without a pharyngeal sucker, the ceca extending almost to the posterior end of the body.

The oral sucker is protrusible and retractile; it may be extended until it is almost wholly outside of the body and retracted until it lies entirely within the body. In this retracted condition it is pyriform, the broader end is anterior and flush with the adjacent surface of the body. Ordinarily the sucker is oval, and about one-half protrudes from the anterior end of the body. The organ is usually a more elongated oval in smaller specimens and relatively broader in larger ones, but it is almost as large in small individuals as in the largest worms.

The oral sucker opens into the long esophagus, which extends posteriorly to the bifurcation of the alimentary tract, about one-fourth to one-fifth of the length of the worm from the anterior end. In a fully extended specimen the esophagus is a straight tube, but on contraction



of the anterior end it manifests a sinuous or spiral course with three or four bends in the anterior two-thirds of its length, while the posterior third or fourth is expanded and straight. Immediately behind the oral sucker the wall of the esophagus is frequently covered with minute spherical evaginations, which communicate with the lumen of the canal and often contain decomposing bits of blood. In cross-section (Figs. 14, 15, and 16) there are usually six or more of these at a given level, but they are arranged in somewhat irregular alternate series, and the esophagus is studded with these little papilla-like protrusions which give it a beaded appearance. This peculiarly modified condition of the wall of the esophagus may extend throughout the length of the organ. The anterior portion of the esophagus is surrounded by a layer of gland cells and the dilated posterior fourth or third is enclosed in a large gland formed by increased numbers of these secretive cells. The cells are ovate, the narrower end pointed toward the esophagus, into which their product is discharged. At the posterior end of the esophagus the cells are very numerous, stain deeply, and occupy practically all the space between the esophagus and the dorsal and ventral body walls (Fig. 16). Where the alimentary canal bifurcates there is a small median pocket (Fig. 17), which extends posteriorly and ventrally. An examination of this region gives the impression that the ceca do not arise from the end of the esophagus, but branch from the side walls a short distance in front of the posterior end. The ceca pass laterally for a short distance after their origin from the esophagus, and then rather abruptly turn backward, extending almost to the posterior end of the body. They are unbranched, slightly sinuous tubes, circular in outline or flattened laterally. They are lined with the usual digestive epithelium, the nuclei situated near the basement membrane and with lobed processes extending into the lumen of the canal. Near the posterior end of the body the crura approach each other and lie parallel for a short distance just before their ends. In two specimens in my collection the crura have fused near the posterior end of the body, a condition recalling that in the schistosomes.

The nervous system in this genus is especially prominent, and the principal features are conspicuous in living specimens and whole mounts. The esophageal commissure (Figs. 14 and 15) is large and situated about one-fourth of the distance from the oral sucker to the bifurcation of the alimentary tract. On the commissure, especially at either side of the median line, there are large ganglion cells. The subesophageal commissure is small. From the commissure one larger and two smaller nerves pass forward, and three extend backward. The posterior ventralis is the



largest and extends on the ventral side just lateral to the ceca. In favorably stained whole mounts these branches can be traced almost to the posterior end of the body.

The excretory system has presented unusual difficulties. The pore is terminal or slightly dorsal in position and opens from a small median vesicle. This divides almost immediately into two small elongated flask-shaped vesicles (Fig. 11), which pass forward and laterad almost half the distance to the ends of the intestinal ceca. From these vesicles two collecting ducts pass anteriad, one on either side of the body dorsal to the intestinal crura. They are so small that they can not be followed with certainty in sections, and in the living specimen the dark contents of the ceca prevent observation, so that this fruitful method of tracing the system has been unavailing. The main collecting ducts have been followed in sections about two-thirds of the distance from the posterior end of the body.

At the posterior end of the body, extending from the region of the oötype almost to the posterior end, there is a large coiled vesicle. The contents are fluid, and stain like a secretion, but the significance of the structure is not clear. I have not been able to find an outlet or connecting tubules, but I am inclined to think it is not associated with the excretory system. It may prove to be a lymph receptacle.

The male reproductive system is unique and characteristic. The testes in mature specimens are usually ten in number, arranged in a linear series in the intercecal area. Often they seem to be contiguous and grown together and it is then difficult in specimens mounted *in toto* to distinguish their limits and to determine their number with certainty. In *S. innominata* this is especially true. The testes are roughly oval but more often are irregularly lobed. The shape varies from spherical to ovate, though the testes usually are flattened antero-posteriorly and broader than long. In the same individual there may be great variation (Figs. 2 and 8), the testes manifesting different shapes. In certain species, *S. innominata* and *S. scripta*, they fill the area between the ceca throughout the testicular zone, in others they are much smaller, occupying not more than half the space between the crura. In *S. scripta* they extend forward almost to the bifurcation of the alimentary tract, and in other species there is considerable space between the end of the esophagus and the testes. The posterior testis is usually the largest, and they decrease slightly in size anteriorly.

There is no vas deferens, the posterior testis communicating directly with the large seminal vesicle. This structure is pyriform, widest an-



teriorly; the anterior wall of the vesicle is usually about the width of the posterior testis. It may expand to a width exceeding that of the posterior testis or, in case the vesicle is not distended with spermatozoa gradually diminishes in width. The dorso-ventral measurement usually slightly exceeds the lateral. Anteriorly then the vesicle occupies practically all the space between the ceca and as it passes caudad to the ovarian level turns toward the left. The ovary is situated between the ceca, about the length of the posterior testis intervening between it and the ovary. The seminal vesicle is often marked by a sharp constriction slightly anterior to the middle of the ovary and then is continued as a narrow canal. At the ovarian level the seminal vesicle enters the cirrus sac. This structure is about one-half as long as the seminal vesicle; is oval in shape, about twice as long as broad, with weakly developed musculature. The prostate is reduced or absent. The genital pore is situated beneath the cecum of the left side at about the level of the caudal margin of the ovary. The cirrus opens anterior and median to the opening of the metraterm.

The female reproductive system is relatively simple. The ovary is a spherical, oval or lobed structure situated on the right side of the body a short distance behind the posterior testis. It is usually about the size of the posterior testis, although smaller in *S. innominata* and larger in *S. picta*. The oviduct arises at the posterior median margin of the ovary and passes posteriorly and dorsally. It then turns toward the right and increases in size to form a vesicle, the receptaculum seminis uterinum, which is often filled with spermatozoa. It then contracts to approximately its earlier diameter and passes posteriad, ventrad, and mediad. From this point there branches a large oval seminal receptacle which passes dorsally and near the dorsal wall of the body contracts to form a short Laurer's canal which opens to the dorsal surface (Fig. 19). After the seminal receptacle the oötype passes dorsally and receives the short large duct from the vitelline receptacle. Mehlis' gland is absent or represented by a few cells in the parenchyma around the oötype. The uterine duct continues its course anteriorly and laterally for a short distance and then turns ventrad expanding into the uterine portion. This dilated portion is present even though empty and is followed by the muscular walled metraterm which opens to the surface just below the cecum of the left side (Fig. 12). In certain descriptions of blood flukes in which a single egg is present in the body the statement is made that a uterus is lacking. The histological character of this section of the female reproductive duct in *Spirorchis* is similar to that of the uterus of other



trematodes, and I am inclined to regard the structure as a short but characteristic uterus. Such a condition is present in many polystomes and was described for these forms by the writer (1917, p. 30). The opening of the metraterm is posterior and lateral to that of the cirrus sac.

The vitellaria are voluminous and well developed. They consist of a continuous mass of follicles, which extend from the level of the bifurcation of the alimentary tract almost to the posterior end of the body and lie chiefly in the extracecal areas but enter the intercecal area dorsally and ventrally. At the posterior end of the body and extending forward to the vitelline receptacle, the follicles of the two sides meet in the intercecal region. Just behind the level of the genital pore, ducts from the vitellaria of either side pass mediad ventral to the ceca and unite to form the vitelline receptacle. This structure extends dorsally and anteriorly and discharges into the oötype.

The uterus contains a single egg, oval in shape, without filaments or spines, and provided with an operculum. Usually the egg is voided when the worm is removed from the blood vessel. Normally the eggs are passed into the blood vessels and by means of these channels are distributed to all parts of the body. They are particularly abundant in the lungs, liver, spleen, kidneys and wall of the intestine. On rupturing the capillaries they pass into the tissues and through them, the majority ultimately arriving at the alimentary canal or one of its evaginations, from whence they reach the exterior. The passage of the eggs through the tissue appears to be passive, and in this respect they act as any hard foreign body. Apparently either end of the egg may precede and the undeveloped condition of the embryo inside the shell would in my opinion preclude the idea that the egg exerts an influence determining the direction of its migration. The eggs produce lesions in the tissue, weakening its texture and are slowly pushed through, as the result of the natural movement of the tissue concerned. This procedure certainly involves a long period of time in the case of certain eggs and probably large numbers never reach the outside world, the death of the embryo and disintegration of the egg occurring before elimination can take place. Fragments of shells are often encountered in the tissue and probably are the remnants of eggs that have broken up after the death of the embryo. In other cases undoubtedly many of the embryos die before the egg reaches a channel of communication with the exterior. Such an explanation may account for the relatively large number of eggs that fail to hatch.

Eggs in the uterus or recently voided have a golden-yellow color, almost exactly like the vitelline material. As the egg grows older the shell



becomes darker in color, and the time which elapses between the deposition of the eggs and their passage from the body must vary greatly with different eggs, which undoubtedly accounts for the color differences which exist in any group of eggs recovered from the feces. Some of the eggs are semi-transparent and the embryo can be distinctly seen, while others are so opaque that little can be distinguished. The eggs vary greatly in size and in a single species there is considerable variation. Eggs embedded in the tissues of the host and those voided in the ejecta of the turtles are larger than those in the uterus of the worm, and this condition agrees with that of other blood flukes where the eggs increase in size during their passage through the tissue of the host. How this increase in size is accomplished after the deposition of the shell is not clear to me, although the shell is permeable, permitting exchange of gases during embryonic development and an aqueous solution of methylen blue used in an attempt to differentiate structure in the miracidium penetrated the shell. The increase is probably brought about by the absorption of water and in my opinion the tension produced by the pressure inside the egg is the determining factor in opening the cap. I do not believe that the activity of the embryo is of itself sufficient to open the shell, as I have observed actively moving embryos in eggs which for ten days failed to hatch.

Eggs recovered from the feces have been kept under observation for long periods of time. In order to simulate natural conditions, the eggs were kept in tap water and examined at frequent intervals. That eggs normally hatch in decomposing material at the bottom of ponds or aquaria is evidenced by the fact that most of the eggs at the bottom of jars in which infected turtles have been kept for long periods of time are merely empty shells; the caps are open and the embryos have emerged. This requires in the case of most eggs a considerable period of time. During migration through the tissue development proceeds slowly, probably due to a low oxygen supply and the fact that the tissue, with as high or higher salt content than the egg, prevents the absorption of water. On reaching fresh water a much larger amount of oxygen is available and the absorption of water increases the water content, raising the rate of metabolism and greatly accelerating development.

When the egg leaves the uterus of the worm the embryo consists of a small group of cells surrounded on all sides by droplets of vitelline material (Fig. 27). At this stage the droplets are approximately the same size. Development proceeds and the embryo grows by the decomposition of the vitelline droplets and the utilization of the yolk material.



During this process vitelline fragments are aggregated to form a few large droplets, so that the yolk globules become different in size (Fig. 29). The cells of the larva become differentiated into those forming the body wall and the various internal structures. The anterior end is early distinguishable by the shape of the larva, the development of the anterior papilla, and the appearance of the larger germ cells at the posterior end. By the time the miracidium is half grown, pigment begins to form in the eye spots, and soon afterward the cephalic glands, nervous mass, and flame cells are discernible. Soon the embryo begins to move, due to the contraction of muscle cells differentiating in the body wall. This muscular movement should not be confused with the ciliary movement which is manifested later. The miracidium is capable of considerable movement before the cilia are formed, and after the cilia appear the muscular movements are separate and distinct. The cilia are not developed till late, and then their formation often requires several days.

Due to differences in shape caused by the muscular contraction, it is difficult to give precise measurements of the miracidium. It may elongate until it is as long as the shell or contract until it is almost spherical. In general, a well-developed larva occupies about one-half of the space within the shell. In shape it is ovate, slightly wider anteriorly than posteriorly, but the anterior end narrows sharply and bears a cone-like prominence that is protrusible and retractile. Frequently the circular muscles will contract at two or three different levels giving the embryo a segmented appearance. With the exception of the anterior papilla, the body of the miracidium is covered with long stiff cilia, uniform in size and distribution but not closely set. In general structure, the larva closely resembles that of the schistosomes.

Discussing the miracidia of the human blood flukes, Cort (1919) says:

Functionally the schistosome miracidium appears to have no dorso-ventral or lateral differentiation, since it is round in cross section and revolves on its long axis in locomotion. Structurally, however, this differentiation is very striking. The arrangement of the excretory system and cephalic glands gives a very clear bilateral symmetry. The cephalic glands lie nearer one surface of the body, and the central nervous body and rudimentary digestive sac lie nearer the other. Since the use of the terms dorsal and ventral are meaningless for such a type as this miracidium, I propose that these surfaces be designated respectively the glandular and neural surfaces.

While the statement of Cort regarding these miracidia is entirely correct, it seems that his proposal of new terms to designate the surfaces is unnecessary. In forms with such definite bilateral symmetry, and particularly in the turbellarian flatworms, the side containing the prin-



cipal nervous mass is dorsal, and the desirability of introducing a new terminology appears somewhat doubtful. I see no especial objection to it, however, and it is used in the description of this form.

The anterior papilla has a cap-like tip and the two cephalic glands and rudimentary digestive sac open through it. The cephalic glands are large, filled with a granular material and, as a result of the amount and character of muscular contraction in the embryo, extend posteriorly one-third to one-half the length of the body. Between them there is the rudimentary digestive sac. The cephalic glands extend almost to the body wall on the glandular side and about half-way to the body wall of the neural side. The rudimentary digestive sac is almost in the middle of the body and extends back about one-third of the total length from the anterior end. At about the center of the body on the neural side there is a large ganglionic mass. It is irregular in shape, broader than long; the lateral measurement is about two-thirds the width of the body at that level. It is situated just behind the digestive sac. On its anterior and neural face it bears a pair of eye spots. These structures are cup-shaped, so situated that they open toward the latero-neural surfaces, and their bases are close together on the central nervous mass. They are conspicuously pigmented, especially the rim of the cup, and this gives the peculiar X-shaped appearance. The eye spots are frequently irregular in form, but vary from the shape and pattern just described. At the posterior end of the body, and extending forward almost to the nervous mass, there are a number of large germ cells. On either side of the body, a short distance in front of the eye spots, there is a pore through which I frequently observed the extrusion of droplets of an oily material. These pores are the openings of the anterior ducts, but the course and relation of the ducts and the character of these organs I have been unable to determine. Near the posterior end on either side of the body there is an excretory pore. The course of the excretory tubules I have not been able to trace with certainty, but the flame cells are conspicuous. One pair of flame cells is anterior in position, situated between the eye spots and the lateral wall of the body. The flame cell leads ventrally and the duct passes posteriad on the ventro-lateral margin of the cephalic gland of that side. Behind the cephalic gland cell it turns mediad and dorsad and there unites with the duct from the posterior flame cell of the same side. The posterior flame cells are situated just in front of the excretory pores, and the cilia beat dorsad and forward. As just described, the duct from either cell leads forward to unite with that from the anterior flame cell of the same side. I have been unable to trace the



course of the common duct from the union of the primary tubules to the excretory pore but I do not believe there is a connection between the excretory tubules of the two sides.

With the development of the cilia the embryo becomes increasingly active within the shell; and living, moving embryos have been kept under observation for as long as four weeks without hatching. The larva first moves forward and backward and later rotates on its long axis. This movement increases in rapidity and is accompanied by contractions of the muscles of the body wall so that the embryo assumes various shapes and swims round and round inside the egg. I have been unable to confirm the observation of Ward that "eggs placed in hanging drop cultures hatch out in from 4 to 24 hours after being mounted." Such early emergence from the shell would only occur in eggs that were far advanced in development, and that it is not usual is evidenced by the fact that Ward did not observe the escape of the miracidium from the shell. Only in a few instances have I been successful in breaking open the eggs and securing normal miracidia, although tap water and various salt solutions were tried. The embryos are almost always distorted and soon disintegrate. Such a specimen is shown in Ward's figure of a miracidium just out of the shell.

I have observed the normal emergence of miracidia in watch glasses and one such egg was transferred by a capillary pipette to a slide as the cap started to open. It was drawn and the embryo after escaping was drawn (Figs. 32, 33 and 34). Comparison of these figures with that of Ward will show the difference between normally hatched embryos and those experimentally removed from the shell. The egg figured in hatching had been removed from the feces and kept three weeks in tap water at room temperature. As the cap was forced open the larva slowly emerged from the shell. The opercular opening is small and escape is not easy. The miracidium came out little by little in a jerky manner. This required about ten minutes and, when free from the shell, the larva was surrounded by a viscous material, the former contents of the egg. Although the cilia beat regularly, the miracidium remained beside the shell for at least five minutes. During this time the only motion was that produced by the contraction of the muscles. Then, suddenly the action of the cilia became more powerful and the miracidium began to move forward, rotating on its long axis as it progressed. It swam rapidly, and whenever active swimming was interrupted or it encountered bits of débris the anterior papilla was extended and retracted in a peculiar exploring and penetrating motion. The vigorous ciliary and muscular



activity of the larva and the protrusive movement of the anterior papilla made it easy for the larva to work its way through débris on the slide. In swimming, the body becomes more elongate and occasionally the posterior part is contracted in such a way that a small caudal appendage is formed. Such normally hatched, free-swimming embryos have been observed for four hours without appreciable abatement of their activity.

The life histories of *Sanguinicola* and the human schistosomes have been worked out and their larval stages described. The miricidia enter different species of snails and the cercariæ have forked tails. Consequently, it would seem probable that the miricidia of *Spirorchis* enter snails and that the cercariæ also are forked-tailed. The activity of the miricidia should enable them to travel considerable distance in search of the suitable intermediate host and the motility of the anterior papilla would facilitate penetration into the tissue of the snail. A very real difficulty is encountered however in predicting the type of parthenita. According to Faust (1918), the Furcocercariæ develop in sporocysts and monostome cercariæ develop in rediæ. If the cercaria of *Spirorchis* is a monostome and if it is a forked-tailed form, both of which seem likely, we would have a condition at variance with the general type of development in trematode larvæ. During the past two years I have made repeated collections of snails from a pond near New York in which practically every specimen of *C. picta* is infested with *Spirorchis*. Three species of snails, *Planorbis trivolvis*, *Physa ancillaria* and *Lymnæa columella* are common but I have been unable to find any cercaria whose structure would associate it with these blood flukes.

Since the life history and developmental stages of these forms are unknown, specific determination of material collected has presented many difficulties. The specimens of this genus that I have examined may, however, be placed in five different groups, which do not seem to intergrade and which I regard as distinct species. *Spirorchis innominata* becomes the type of the genus. Although the description of Ward in my opinion includes more than one species, his figure and the majority of his data agree with one of my groups and for that form I would retain the specific name *artericola*. For the other three species I propose the names *S. elegans*, *S. scripta* and *S. picta*. Comparison of the figures will give the best idea of the likenesses and differences between the species. *S. innominata* is larger than the others; the testes are larger and less distinct from one another; the oral sucker is relatively smaller; the esophagus is shorter; and the genital pore is near the posterior end of the body. The other species are slightly smaller and differ in many structural features.



In *S. artericola* the testes are smaller, more distinct, and occupy the posterior two-thirds to three-fourths of the region between the bifurcation of the alimentary tract and the ovary; and the genital pore is much nearer the posterior end of the worm. In *S. elegans* the similarity to *S. artericola* is pronounced but the oral sucker is larger; the testes are less distinctly separated from one another; and the genital pore is considerably farther forward than in *S. artericola*. *Spirorchis scripta* is usually more pointed at either end; the oral sucker is larger; the testes are very large and extend forward almost to the bifurcation of the alimentary tract; the genital pore is relatively far forward; and the large vesicle at the posterior end of the body is especially prominent. In *S. picta* the testes and ovary are almost spherical; the lobulations characteristic of other species are reduced or absent; the testes are small, much smaller than the ovary, often distinctly separated; and the ovary is larger than in any of the other species.

Due to the variation in size of eggs and their increase in size during their passage through the tissues, I have not used the size of eggs as a distinguishing character. If eggs *in utero* only are considered, it might prove a valuable characteristic, but the egg in the uterus may not be completely developed and, if ready for oviposition, is usually voided when the fluke is removed from the vessels. Consequently, egg measurements might easily prove confusing. The vitellaria are not divided into discrete lobes; the follicles form a continuous mass and, while there are slight differences in these structures, they do not seem well adapted to serve as a means of specific distinction.

***Spirorchis innominata* Ward, 1921**

Plate II, Figure 1

This species at present is known by three specimens mounted *in toto*, the most characteristic of which I have shown in Fig. 1. This is the specimen designated by MacCallum as type, and the measurements of the specimen are, I believe, representative. The other specimens are about the same size and, although bent and slightly distorted, agree in diagnostic features. The type specimen manifests those features described as characteristic of the genus. This worm is 4 mm. long and 0.66 mm. in width near the middle of the body.

The oral sucker is oval, longer than broad, and measures 77 by 54 microns. The esophagus passes posteriad in spiral fashion, the coils elongating and enlarging posteriorly. There are five of these turns, the hinder one much straightened. The esophagus is narrow at its origin



from the oral sucker and gradually widens through the first third of its course. Here it is crossed by the commissure of the nervous system. The region posterior to the commissure is broader, measuring 60 microns in width. In total length the esophagus measures 0.64 mm. Its anterior portion is surrounded by a layer of gland cells, giving it a beaded appearance, and at the posterior end for a distance of 0.26 mm. there is a deeply staining mass of these cells around the esophagus. The origin of the intestinal diverticula is well shown in the figure. The ceca slightly exceed the esophagus in width, have lobed or crenated walls, and extend almost to the posterior end of the body. They are filled with decomposing blood, which gives them a black color, and the ends of the ceca approach each other but do not fuse.

The ovary is situated a little to the right of the median line, about one-third of the distance from the posterior testis to the end of the body. It is lobed, about 0.17 mm. in diameter, and the oviduct arises at its median posterior margin. After about 0.09 mm. it expands into the receptaculum seminis uterinum, which passes posteriad on the right side of the body. The seminal receptacle is about as long as the narrow portion of the oviduct and then it is obscured by the large transverse duct from the vitellaria. The vitellaria extend as a mass of follicles from the level of the posterior part of the esophagus to the posterior end of the body. They are principally extracecal in position, but extend into the intercecal areas anterior and also posterior to the other reproductive organs. About 0.42 mm. from the posterior end of the body vitelline ducts pass mediad from either side to form a common reservoir. The connection of the vitelline duct with the oötype can not be distinguished, but from this region the uterus passes forward ventrally and laterally to the genital pore. In the uterus there is an egg which measures 77 by 48 microns. I have examined many individuals of *Clemmys insculpta* in the attempt to find worms of this species in the blood vessels. Although I have not been successful in securing adults, I have found eggs in the tissue and in the feces which I believe belong to this species. In the tissue they are slightly larger than the one present in the specimen here described, and eggs in the feces containing living miracidia have an average measurement of 108 by 85 microns.

The testes were described by MacCallum as a rough spiral column almost filling the whole cavity between the ceca. He distinguished an anterior conical mass and nine other irregularly shaped masses. They begin 0.38 mm. behind the bifurcation of the alimentary tract and extend to within 0.95 mm. from the caudal end of the body. The seminal



vesicle as described by MacCallum is conical in shape, its base flush with the posterior face of the last testis, and its apex directed posteriad, ventrad and sinistrad. It passes underneath and at the left of the anterior median margin of the ovary. The cirrus sac in this specimen is rather small and opens at the genital pore located beneath the cecum of the left side 0.47 mm. from the posterior end of the body.

Type host, *Clemmys insculpta* (syn. *Chelopus insculptus*).

This species resembles *S. artericola* in the position of the genital pore and *S. scripta* in the massive character of the testes. It differs from *S. elegans* and *S. picta* in both of these features.

### ***Spirorchis artericola* (Ward), 1921**

Plates IV to VIII, Figures 7-36

This form was described by Ward as the only species parasitic in the vascular system of various fresh-water turtles. He was unable, however, to make his description cover all his material and clearly was not satisfied with his conclusion. I have restricted the specific description to a group of specimens collected from the heart and arteries of *Chrysemys marginata*, *C. picta*, and *Pseudemys scripta* which have uniform and common characters.

Adult worms (Figs. 7 and 8) vary in size from 1.4 by 0.24 to 2.84 by 0.67 mm. As described by Ward, the body is an elongated oval, with the anterior end more nearly pointed and much more mobile than the posterior, and it is often slightly concave on the ventral side. It is relatively thin, but I find the dorso-ventral measurement considerably greater than stated by Ward. He gave the thickness as varying from 70 to 80 microns and, while I have specimens equally thin, others measure as much as 170 microns in thickness. The oral sucker is oval, longer than broad, and measures from 60 to 78 microns in length and from 42 to 60 microns in width. The esophagus is on the average about one-fifth as long as the body and has the usual gland cells around it. The ceca have no peculiar features and vary in diameter depending on the amount of material they contain.

The testes are usually ten in number. They are irregular in shape, oval or lobed, and form a regular consecutive series just behind the center of the body. The testicular area occupies about one-fourth of the width of the body, and from one-third to one-half of the length of this area intervenes between the anterior testis and the bifurcation of the alimentary tract. The two or three anterior testes are situated in the anterior half of the body and the seven or eight are located in the posterior



half. The distance between the caudal testis and the posterior end of the body is about two-thirds of the distance between the cephalic testis and the anterior end of the body. The seminal vesicle is conical or pyriform, situated immediately behind the caudal testis. The wider end is anterior, and posteriorly it passes underneath the anterior median part of the ovary. This posterior part narrows to a small duct which communicates directly with the cirrus. The cirrus sac is small, the muscles of the sac weakly developed. As pointed out by Ward, the vesicle and duct form a nearly straight passageway from the posterior testis to the genital pore.

The ovary is a many-lobed organ, situated slightly at the right of the median line a short distance behind the testes. It is somewhat dorsal in position and about one-sixth to one-seventh of the body length from the posterior end. It varies considerably in size. In the smallest sexually mature specimen it measures only 67 to 78 microns and in the largest 190 by 190 microns. The character and extent of the vitellaria are well described by Ward:

The yolk glands are exceedingly voluminous. They begin at about the end of the esophagus and extend just a little beyond the posterior ends of the intestinal crura. The cells though not crowded form an almost continuous strip or band which lies below, and to some extent, on both sides of the crura but only in the immediate proximity to those structures, for the central area of the body is entirely without yolk cells. At the end of the esophagus and behind the crura, the cells from the two sides approach and become confluent in the median line. Behind the ovary on the ventral side of the body, the transverse yolk duct joins the two yolk glands and on it in the median line is formed a prominent yolk reservoir.

The ducts of the female system show no marked variation from type usual in the genus. The genital pore is situated below the cecum of the left side about one-seventh of the body length from the posterior end. The eggs vary considerably in size. One present in the uterus of the smallest sexually mature specimen measures 50 by 35 microns and eggs in the uteri of larger worms measure as much as 75 by 60 microns. The average size of a large number of eggs taken from the feces and containing living miracidia was 86 by 74 microns, although there was considerable variation from these figures.

This species has been found in *Chrysemys marginata*, *C. picta* and *Pseudemys scripta*.

It resembles *S. innominata* in the relative position of the reproductive organs and genital pore, but the oral sucker is larger, the ovary is larger, and the testes are smaller.



**Spirorchis scripta**, new species

Plate III, Figures 4, 5

The material of this species consists of one specimen from *Graptemys pseudogeographica* (syn. *Malacoclemmys leseurii*) collected near Newton, Texas, and several others from *Pseudemys scripta* collected near Raleigh, North Carolina. The first specimen was taken December 15, 1913, from the trachea of *G. pseudogeographica*. At that time the true character of the worm was unknown, but the card recording the dissection bears the following note: "This worm moves rapidly by a peculiar flapping or wriggling movement of the lateral edges and also by rapid contractions and elongations. It contracts till very short and then extends a long slender anterior portion. The movements are very rapid and violent, although graceful. Monostome; rather long esophagus with nerve commissure and two trunks running forward and two backward extending laterally almost to the posterior end of body. Ceca with dark contents. Genital organs between ceca, single egg in body." This worm was then stained and cut in serial sections. The next specimen was found November 10, 1914, in the washings of the dissected intestine of a specimen of *Pseudemys scripta* collected near Raleigh, North Carolina. This worm undoubtedly came from the mesenteric vessels. It was stained and mounted *in toto*. Later dissections revealed the true nature of these worms, and on October 21, 1916, twelve additional specimens were removed from the heart and arteries of another specimen of *P. scripta* from Raleigh, N. C.

These worms are almost fusiform in outline; the reproductive organs are large, situated nearly in the middle of the body; and the anterior and posterior ends taper uniformly to rather pointed tips. They vary in length from 1.15 to 1.66 mm. and in width from 0.23 to 0.35 mm. The body is very thin, in one specimen cut in cross-sections it measures only 54 microns in greatest thickness.

The digestive system is of the usual type but marked by the large size of the oral sucker and the small caliber of the intestinal crura. The oral sucker is oval, longer than broad, and measures from 64 by 46 microns to 77 by 54 microns. The esophagus is narrow where it joins the oral sucker and increases in width in the anterior half. The posterior half is of an almost uniform diameter. It is slightly sinuous in preserved specimens and surrounded by the characteristic glandular cells. The enlarged portion of the gland encloses the posterior third of the esophagus. The median pocket, which extends posteriad and ventrad from the bifurcation of the alimentary tract, is large and conspicuous, reaching almost



to the anterior testis. In all the specimens the ceca are small and almost uniform in diameter. These blind tubes undoubtedly vary in size and may be distended by the presence of large amounts of blood, but in this species they seem to be appreciably more slender than in others.

There are ten testes, forming an almost solid column between the ceca from the posterior end of the esophagus to the seminal vesicle. The testes are large, irregularly oval or lobed, and not always distinctly separated from one another. The testicular area is situated almost exactly in the middle of the body and extends about two-fifths of the total body length. The testes are flattened antero-posteriorly and measure from 80 to 100 microns in width and from 40 to 80 microns in length. The seminal vesicle and cirrus sac conform to the regular pattern and show no peculiar variations. The genital pore is situated about one-fourth of the body length from the posterior end, and in this respect is quite different from the condition in *S. innominata* and *S. artericola*. Not only is the genital pore relatively farther forward, but the other reproductive organs, testes, ovary, and oötype are correspondingly more anteriad than in the other two species.

The ovary is deeply lobed, about the size of one of the testes, and separated from the caudal testis by slightly less than its width. It is situated at the caudal end of the penultimate fourth of the body. The oviduct arises at the posterior median margin and passes dorsad and dextrad. It soon expands and the enlarged portion is filled with spermatozoa. This section of the genital duct passes posteriad and the oötype is about the diameter of the ovary behind it. The vitellaria occupy the usual position, extending from the level of the bifurcation of the digestive tract almost to the posterior end of the body. Their ducts pass mediad at the level of the oötype to form a common reservoir, which discharges into the oötype just left of the median plane. Immediately before the opening of the vitelline receptacle and slightly right of the median plane, the seminal receptacle branches from the oötype and following an expanded vesicular portion a short Laurer's canal opens to the dorsal surface in the median line. The opening of this canal is behind the vitelline receptacle. Eggs in the uterus vary in size from 65 by 38 microns to 77 by 46 microns.

This species has been found in *Pseudemys scripta* from Raleigh, N. C. and in *Graptemys pseudogeographica* from Newton, Texas.

It resembles *S. innominata* in the large size and massed arrangement of the testes, but is much smaller and the genital pore is farther forward.



**Spirorchis elegans**, new species

Plate II, Figures 2 and 3

The material of this species consists of two worms taken from the washings of dissected intestines of *Pseudemys elegans* collected near Havana, Illinois. One was found on November 5, and the other on November 18, 1913. Both were stained and mounted *in toto* (Figs. 2 and 3). These two specimens differ so markedly from all others I have examined that they can not be assigned to any of the other groups and I regard them as representatives of a separate and distinct species. The first one found (Fig. 3) is much contracted and flattened but, on comparing the two specimens, the relative position and relationship of structures are strikingly constant and this agreement shows that features like the position of the genital pore, location and extent of testes, as well as size of the various organs, do not vary greatly with the degree of contraction and may well serve as specific criteria. The longer of the two specimens is designated as type and the species is based on its description. Measurements of the other are included for comparison.

In shape the type specimen is an elongated oval, widest at about the middle of the body. The contracted specimen is oval, slightly wider anteriorly, with somewhat pointed extremities. The longer worm measures 1.71 mm. in length by 0.41 mm. in extreme width, the shorter is 1.15 by 0.62 mm.

The oral sucker of the type specimen is 73 microns in length and 62 microns in breadth; that of the contracted worm is 54 microns in length and 81 microns in breadth. The esophagus extends through about one-sixth of the body length and conforms to the pattern typical for the genus. The large glandular mass surrounds the posterior third of the esophagus. The intestinal crura are comparatively large and their course is very sinuous.

The testes are not distinctly separated from one another and it is difficult to distinguish their limits with certainty. In the contracted specimen they appear to form follicles in a single testis, but in the longer specimen the ten testes may be recognized. The testes are deeply lobed, and consequently it is difficult to give precise measurements of individual testes. The group of testes is situated nearly in the middle of the body and extends through slightly less than one-third of the length of the worm. At the center of the series the testes measure 106 microns in width, while at the anterior and posterior ends the testes are only about 70 microns in width. The distance from the cephalic testis to the bifurcation of the alimentary tract is two-thirds the length of the esophagus.



The seminal vesicle and cirrus sac are clearly visible, as shown in the figures. The genital pore in both specimens is one-fourth of the body length from the posterior end, and this ratio thus appears to be constant.

The ovary is conspicuously lobed, slightly larger than any one of the testes, and situated relatively close to the caudal testis. It is on the right side, immediately in front of the level of the genital pore. The oviduct and vagina are visible in both specimens but the vitelline ducts and receptacle make it difficult to determine the details of the oötype in the whole mounts. There is, however, no indication that there is any variation from the usual form. The vitellaria extend from the level of the bifurcation of the esophagus almost to the posterior end of the body and in front of the testes and behind the vitelline receptacle occupy the region between the ceca. Neither specimen contains an egg.

Type host: *Pseudemys elegans*.

In position of genital pore this species agrees with *S. scripta* and *S. picta* but differs from both in the size and character of the testes. In the confluent form of the testes it resembles *S. innominata*, but the testes are much smaller and the genital pore is farther forward.

### ***Spiorchis picta*, new species**

#### Plate III, Figure 6

This species is represented by four worms taken from the arteries of *Chrysemys picta* collected in the vicinity of New York City. While these specimens have definite spirorchid characters and certainly belong to this genus, they manifest marked differences from all other members of the genus and especially from *S. innominata*, the type species.

The first difference noted is in the shape of the body. These worms have rounded posterior and pointed anterior ends, while the sides of the body throughout most of its length are nearly parallel. The region of greatest width is at or slightly anterior to the center of the body. The largest specimen is 2.33 mm. in length and 0.47 mm. in width, the smallest is 1.48 mm. in length and 0.35 mm. in width.

The oral sucker is large, oval in shape and longer than broad. It varies in size from 0.046 by 0.038 mm. in the smallest individual to 0.077 mm. by 0.054 mm. in the largest. The remaining portions of the alimentary tract are similar in essential respects to those of other species, but the ceca are large and comparatively straight.

It is in the reproductive organs that the species differs most markedly from *S. innominata*. The testes are small, distinctly separated, and frequently there is considerable of an interval between them. They



are lobed, but the indentations are very shallow and under low magnification they appear to be round. With the exception of the one or two most anterior testes they do not differ much in size. In one specimen they are all 35 microns in diameter; in the specimen shown in Figure 6 the largest testis is 60 microns in diameter and the cephalic testis is very small, measuring only 30 microns in diameter. The testes are situated almost in the center of the body, the cephalic testis about one-third of the body length from the anterior end, the caudal testis about one-third from the posterior end. There is considerable space between the testes and the ceca, and the vitellaria extend into the intercecal area on both sides of the testes throughout the testicular region. This condition is not present in any other species in the genus. The seminal receptacle is of the usual pyriform shape, larger than any one of the testes, and the genital pore is situated one-fourth of the body length from the posterior end.

The ovary is very large, faintly lobed, but almost spherical. In the smallest specimen it is 0.1 mm. in diameter and in the largest it is 0.2 mm. In the specimen shown in Figure 6 it measures 0.17 mm. The ovary has a diameter about three times that of any of the testes, a prominent feature characterizing this species. The ovary is pressed against the cecum of the right side for a considerable distance and closely approaches the cecum of the left side. The oviduct is short, and the structures of the oötype are compressed into a small area. The genital pore is slightly anterior to the level of the caudal margin of the ovary. The vitellaria are extensively developed and lie on both sides of the ceca throughout their length in front of the ovary and behind the vitelline receptacle. Eggs in the uterus average 77 by 54 microns in size.

Type host: *Chrysemys picta*.

In the position of the genital pore this species agrees with *S. scripta* and *S. elegans*, but it differs from both these species in the relative size of ovary and testes.

#### Key to the Species of *Spirorchis*

- 1 (4). Genital pore one-seventh of body length from the posterior end.....2.
- 2 (3). Testes larger than ovary, not distinctly separated.....*S. innominata*.
- 3 (2). Testes smaller than ovary, distinctly separated.....*S. artericola*.
- 4 (1). Genital pore one-fourth of body length from the posterior end.....5.
- 5 (6). Testes large, extend to bifurcation of alimentary tract.....*S. scripta*.
- 6 (7). Testes large, do not extend to bifurcation of alimentary tract....*S. elegans*.
- 7 (6). Testes small, not more than one-half the size of the ovary.....*S. picta*.



**HENOTOSOMA** Stunkard

A preliminary description of this genus was published by the writer (1922) and *Henotosoma hæmatobium* was described as a new species and the type of the genus. In the genus was included provisionally *Spirorchis chelydræ*, a species reported by MacCallum at the meeting of the American Association for the Advancement of Science held in December, 1921, but not as yet fully described. MacCallum's report (1922) states:

Only July 17, 1921, I found within the heart of a *Chelydra serpentina* (western form) five Spirorchidæ which were attached to the walls of the ventricle, but all coiled together as if in coition. These worms were the largest of any Spirorchidæ I had seen, being in length 8.50 to 9 mm.  $\times$  1 mm. wide, and which I have named *S. chelydræ*. The peculiarity about these worms is the much bent esophagus, also the numerous glands at the junction of the esophagus and ceca and possibly posterior also on the outside of the esophagus to the mouth.

The statement of MacCallum is so brief and indefinite that it is hardly possible to recognize a species from his description. The last sentence would indicate that the mouth is posterior, which certainly is not the case. The only data in his report upon which a specific determination could be based are size and location in the host. All members of the family Spirorchidæ, as far as known, may be found in the heart; the course of the esophagus depends upon the amount of extension or contraction in the anterior part of the body; and the esophageal glands mentioned are characteristic of blood flukes in general. Consequently, these features can not serve as specific criteria. Accordingly, I wrote to Dr. MacCallum asking for a loan of the material which, although his description had not yet been published, he very kindly forwarded for examination and comparison. None of the specimens were in good condition. In the only specimen that had not been cut in two, the posterior half of the body was crushed and the testes shattered. The specimens examined manifested the general features designated as characters of the genus *Henotosoma* but in certain particulars they differed from those I had collected and I was unable to include them in the same species. So I described the worms I had collected as a different species, assigned to them the specific name *hæmatobium*, and included MacCallum's form as a second species in the genus *Henotosoma*. In a letter received from Dr. MacCallum shortly after the appearance of the paper, he stated that in his opinion the two forms are identical. He gave no reason for the belief and has not published a final description of his species. In the specimens sent to me the testes are not distinctly separated and are deeply lobed; the indentations are so prominent that the organs have a dendritic appearance and, in my judgment, at least until further evidence is submitted, the two species should be retained.



This genus is characterized by the small oral sucker and relatively short esophagus; absence of pharynx; terminal excretory pore and excretory vesicle which divides almost immediately to form lateral collecting ducts; testes usually ten in number, irregularly lobate or sinuate, arranged in a linear series anterior to the ovary but situated in the posterior half of the worm; seminal vesicle posterior to the testes with only the terminal part of the ejaculatory duct enclosed in a small cirrus sac; genital pore ventral, sinistral, near the posterior end of the body; vitellaria numerous, extending from the bifurcation of the alimentary tract almost to the posterior end of the body; seminal vesicle and Laurer's canal present; uterus short, eggs discharged singly.

***Henotosoma hæmatobium* Stunkard, 1922**

Plate IX, Figures 37 and 38; Plate X, Figures 39 to 44

The generic characters are based on a study of *H. hæmatobium*, the type species. Infection by this species is widespread, extending from the Mississippi Valley eastward to New York and the southern Atlantic states. As a parasite of *Chelydra serpentina*, its distribution probably corresponds with that of its host. The percentage of infection is also great, at least one-half of these turtles that I have examined have had eggs in the tissue and in a considerable number live worms have been found in the vascular system. The first specimen was found December 1, 1914, in the lung of a large turtle collected near Raleigh, North Carolina. In the fall of 1916, six specimens were removed from the left subclavian artery of another turtle belonging to this species and collected in the same locality. Since that time, other specimens have been removed from the heart and larger arteries of turtles collected in New York and New Jersey. In November, 1921, a shipment of twelve turtles was received from North Judson, Indiana, and nine were infected. Records of dissection in this group show one turtle in which twelve specimens were found in the lungs, four in the pulmonary arteries, two in each auricle, sixteen in the ventricle, eight in the mesenteric arteries, and twenty-eight at the posterior end of the aorta. This is the heaviest infection with blood flukes that I have ever encountered and the presence of such a large number is probably unusual. Usually, the number of these parasites present in a single host is small, the average of dissections is five or six. Where several worms have been found together, they were often entangled and very hard to separate. Those found in the ventricle of the heart frequently were partially embedded in the wall.



The infection persists for a very long period of time. Living worms have been removed from the arteries of turtles kept in the laboratory over a year, during which time there was no opportunity for them to acquire new trematode parasites, and the eggs remain in the tissues for a much longer period. It is difficult to see how eggs from certain parts of the body could ever reach the outside world, and the disintegration and removal of the shell following the death of the embryo is probably only slowly accomplished. Consequently, considering the longevity of the adult parasite, it seems likely that traces of a single infection might remain for several years. As in the genus *Spirorchis*, the eggs are deposited singly in the blood vessels, and I regard it as very unlikely that the flukes visit the heart for oviposition, since the eggs are probably formed continuously and discharged almost immediately. The worms undoubtedly resort to the heart at times and may sometimes remain there, when the eggs might be carried by the circulation to any part of the body. In fact, all the tissue becomes infiltrated with eggs if the infection is heavy, but usually most of the eggs are found in the tissue of the visceral organs.

These worms are elongate, flattened monostomes with almost parallel sides, rounded posterior and pointed anterior ends. The anterior end in extended condition narrows uniformly to the tip and may be exceedingly slender (Fig. 38). On contraction it may form a sharp angle or become broad and blunt with crenated margins (Fig. 37). The esophageal section appears to be much more mobile than the rest of the body. Extended individuals are widest in the region of the testes and have a narrow zone in the central part of the body. In a contracted condition the body anterior to the testes becomes approximately the width at their level. Living worms may extend to a length of 12.5 mm. and contract to less than 6 mm. Although this form is much more massive than *Spirorchis* and probably more powerful, its movements are slow and I have never witnessed the rapid contractions frequently shown by *Spirorchis*. Fixed and mounted specimens measure from 5 to 9 mm. in length and from 0.48 to 0.75 mm. in width. The width is from two to three times the dorso-ventral measurement, and varies with the amount of contraction.

The cuticula is thin and smooth, lacking spines or other modifications. In sections, the surface of the body both dorsally and ventrally is sometimes irregularly studded with small droplets of what appear to be a secretion. These globules do not stain with ordinary methods and their significance is uncertain.



The oral sucker is situated at the anterior tip of the body and is capable of considerable extension and retraction. In extended specimens it slightly protrudes from the body. It is ovoid in shape, wider anteriorly, and measures from 0.077 to 0.1 mm. in length and from 0.071 to 0.084 mm. in width. The mouth opening is subterminal. Depending on the amount of contraction in the anterior region of the body, the esophagus is slightly or exceedingly sinuous, the sinuosity varying with the extent of contraction. In length it measures from 0.39 to 0.77 mm. It increases in diameter posteriorly although the size of the lumen is not uniform; frequently there are one or more dilated portions. In cross-section the wall has a crenated appearance (Fig. 39), the lining is cuticular and throughout its length the esophagus is surrounded by gland cells. At the posterior end, for about one-fifth of its length these secretive cells are larger, more numerous and form a conspicuous, deeply staining gland, (Fig. 37). No pharynx is present. The posterior end of the esophagus forms a sac or pouch which extends caudad and ventrad from the origin of the ceca. Its lining is cuticular like the esophagus, and it is filled with disintegrating food material. The intestinal crura arise just before the posterior end of the esophagus and pass laterad about one-half of the distance to the body wall, where they turn sharply posteriad and extend almost to the posterior end of the body. Their course is notably sinuous, and they are spread farther apart in the region of the testes and ovary, passing lateral to these organs. They have an almost uniform diameter and are usually filled with decomposing blood, which gives them a black appearance. The crura are lined with a single layer of epithelial cells resting on a basement membrane. These cells have broad lobate processes that extend into the lumen of the ceca and their nuclei lie close to the basement membrane. The cytoplasm is filled with dark granules, derived from the decomposition of blood. These granules in the intestinal epithelium clearly demonstrate the nature of their food and show that they live on the blood of the host.

The excretory pore (Fig. 44) is situated at the posterior end of the body and the vesicle divides almost immediately to form two lateral collecting ducts which pass anteriorly. In spite of repeated attempts, I have been unable to trace these vessels in living specimens, and their small size, together with the vacuolated character of the parenchyma, has thus far made it impossible to follow them in sections.

Near the posterior end of the body, extending in the median line from the level of the vitelline receptacle almost to the excretory pore, there is a much coiled vesicle (Fig. 44). A similar structure was described in



*Spirorchis*. It is filled with a fluid substance that takes a plasma stain, but its connections and relations are uncertain.

The nervous system in essential features resembles that of *Spirorchis*. Due to the greater thickness of the body the main trunks are not so prominent, but may be easily seen in whole mounts. The esophageal commissure is situated about one-fourth of the distance from the oral sucker to the bifurcation of the alimentary tract, and the principal pair of anterior nerves pass forward on either side to the oral sucker. The posterior ventral nerves are the largest and extend backward just lateral to the ceca.

The male reproductive organs are located in the posterior half of the worm. The testes lie, one behind the other, in the intercecal area. In mature specimens there are ten, but as the period of sexual activity declines certain of the testes disintegrate and disappear. In one turtle kept for over a year in the laboratory four of the seven flukes found show this condition. The posterior testis remains but the ones immediately in front of it break up. One specimen has the anterior six testes and the last; another (Fig. 38) has the anterior four and the last. How long before this situation develops can only be surmised, as there is no way of knowing how long these flukes had been in the blood vessels before the hosts were taken. In these specimens the ovary appears to be filled with cells and actively functional, showing no sign of exhaustion. The anterior testes have prominent lobes and are distinctly separated, while in the middle of the group the lobulations are smaller, less conspicuous and the organs closer together. The testes are flattened antero-posteriorly and this is particularly noticeable at the center of the group where the pressure is greatest. Because of their shape it is difficult to make satisfactory measurements of the testes, but they vary in size from 0.12 by 0.27 mm. to 0.27 by 0.43 mm. In the testicular area they occupy practically all the space between the ceca, but do not extend laterally beyond them. The most anterior testis is about three-fifths of the body length from the anterior end and the caudal testis about one-sixth of the body length from the posterior end. The posterior testis opens directly into a large ovoid or pyriform seminal vesicle. The broader end is anterior and the posterior end tapers to a duct which passes on the left side of the body and near the mid-ovarian level enters the cirrus sac. This sac is small and the muscular wall slightly developed. It is pyriform in shape, wider anteriorly, and a prostate is reduced or absent. The cirrus sac varies in length from 0.154 to 0.22 mm. and in width from 0.05 to 0.077 mm. The genital pore is ventral, beneath the



cecum of the left side and about the level of the caudal margin of the ovary. The opening of the cirrus is anterior to that of the uterus and the cirrus is eversible (Fig. 42).

The ovary is a lobed, oval structure situated on the right side of the body between the seminal vesicle and the genital pore. It measures from 0.154 by 0.22 mm. to 0.23 by 0.28 mm. It is oblique in position; its forward end is anterior and at the right; its posterior end caudal and median. The oviduct arises at the median posterior margin and passes dextrad and posteriad. After continuing for a short distance it turns mediad where the seminal receptacle and Laurer's canal are given off and immediately afterward the common vitelline duct is received. The oötype region is short; no Mehlis gland was observed; and there is a distinct uterus (Fig. 44), which shows clearly even though empty. The metraterm passes forward, sinistrad, and ventrad to the genital pore. The vitellaria are enormously developed, and consist of masses of follicles extending from the bifurcation of the alimentary tract almost to the posterior end of the body. They are not separated into lobes but form an almost continuous sheet of cells extending on the lateral side of the crura throughout their length and filling the intercecal area anterior to the testes and posterior to the vitelline receptacle. Wherever there is any space between the testes or the ovary and the intestinal crura, vitelline follicles have grown into the intercecal area. Just behind the level of the genital pore vitelline ducts pass mediad on the ventral side of the body and unite to form the large vitelline receptacle which discharges into the oötype. The uterus is short and contains a single oval egg. The eggs are thick shelled, and golden brown in color. The smallest egg measured in the uterus is 0.077 by 0.06 mm. and the largest 0.086 by 0.065 mm. Eggs in the tissue of the host are larger and those taken from the feces have an average measurement of 0.115 by 0.081 mm. The eggs grow darker with age. They have an operculum (average size 22 microns in diameter) to permit the escape of the embryo. The eggs of this form are longer, more rectangular, and develop more slowly than those of *Spirorchis*. Most of the eggs taken from the feces contain an embryo that is still an oval mass of cells enclosed in vitelline globules. The development of the larva is like that of *Spirorchis* and the miracidia of the two forms are so similar that it would be exceedingly difficult to distinguish them when freed from the shell.

Type host: *Chelydra serpentina*.



**HÆMATOTREMA**, new genus

A new genus, *Hæmatotrema*, is formed to contain a new species of blood flukes found in the arteries of *Chrysemys picta*. This genus manifests the characteristic features of the subfamily Spirorchinæ and constitutes a third genus in that group. The generic description may be stated as follows.

Exceedingly small and slender monostomes with delicate body which tapers toward both ends. Oral sucker large, elongate, protruding; relatively long esophagus with esophageal glands not strongly developed; intestinal crura sinuous, extending almost to the posterior end of the body. Testes lobed, four or five in number, situated in the anterior part of the posterior half of the body; seminal vesicle between testes and cirrus sac; genital pore below the cecum of the left side, one-fourth of the body length from the posterior end. Ovary lobed, on the right side, at or slightly anterior to the level of the genital pore; vitellaria envelop the ceca throughout their length and fill the intercecal area anterior to the testes and posterior to the oötype; seminal receptacle and Laurer's canal present; uterus short, eggs very large, operculate, discharged singly.

**Hæmatotrema parvum**, new species

Plate XI, Figures 45 to 49

Twenty five worms of this species have been stained and mounted either entire or in sections and many others have been lost in manipulation. All the material came from the blood vessels of *Chrysemys picta* collected near Cold Spring on the Hudson, New York. Most of the specimens were found in the normal salt solution in which the organs were dissected. They are too small to be readily observed in the tissue or in the arteries and are usually found only when freed in the dissection fluid. In several instances, however, in which the heart and arteries were removed from the body of the host and examined separately, specimens were found in the arteries while teasing these vessels open with needles under a binocular. The largest number obtained from a single turtle was six, although, since they are so small, it is probable that others were present in the tissue and unnoticed. In this species, as in other blood flukes, it appears probable that the infection is light and the number of parasites small.

The specimens vary in size from 2.2 by 0.12 mm. to 0.75 by 0.05 mm. The relative length to width is about ten to one and the thickness is about one-half the width, although these proportions represent a mean about which there is considerable deviation as the body is extended and contracted. The posterior end is not so mobile as the anterior and is usually rounded, while the anterior end is capable of considerable extension and in this condition becomes narrow and tapering. The greatest width is usually in the region of the testes, although some of the specimens have a widened spatulate region near the posterior end of the body.



The cuticula is very thin and the muscular wall of the body extremely delicate.

The oral sucker (Fig. 46) is large and elongate. It is ovoid in shape, wider anteriorly, and varies in size from 0.073 by 0.035 mm. in the largest specimen to 0.052 by 0.027 mm. in the smallest. The sucker protrudes slightly from the body and the mouth is subterminal. The digestive system conforms to the type present in *Spirorchis* and *Henotosoma*. The esophagus is long, extending through one-fifth to one-sixth of the body length and it becomes sinuous with the contraction of the anterior end of the body. It is lined with cuticula; the lumen is relatively large, increasing in size posteriorly although the diameter frequently is not uniform and dilated portions are present. Throughout its length it is enveloped by secretive cells, which are larger and more numerous posteriorly, but these cells are not so numerous or prominent as in *Spirorchis* or *Henotosoma*. The posterior end of the esophagus turns ventrally, forming a small median pocket, and the ceca diverge at right angles from the esophagus immediately in front and above the median diverticulum. The crura extend laterally about half-way to the body wall and then bend sharply backward, passing almost to the posterior end of the body where they end blindly. They are small, their diameter hardly exceeding that of the esophagus.

The excretory pore is terminal, the vesicle is very small and two collecting ducts pass forward. The details of the system have not been worked out, but in general form it agrees with that of *Spirorchis* and *Henotosoma*. The excretory system is probably characteristic for the subfamily.

The esophageal commissure and the anterior and posterior ventralis nerves are the only parts of the nervous system visible in whole mounts, and the others are so small that it is very difficult to trace them in sections. So far as I have been able to determine, the nervous system is similar to that of *Spirorchis*.

The testes are lobed, oval or spherical bodies of almost equal size situated in the intercecal area. They are situated one behind the other and are distinctly separated. In about one-half of the specimens there are five testes, in all the others four. They are usually slightly longer than broad and vary from 46 to 57 microns in length, from 38 to 50 microns in width, and from 32 to 44 microns in thickness. The anterior testis is about midway between anterior and posterior ends of the body, and the caudal testis about one-third of the body length from the posterior end. They extend laterally almost to the ceca filling the



intercecal area at the testicular zone. The caudal testis opens into an ovoid or pyriform seminal vesicle, which is about the size of one of the testes. The broader end of the vesicle is forward and caudally it contracts to form a duct which passes at the left of the ovary and enters the cirrus sac. The cirrus sac turns ventrally and opens at the genital pore. The sac is small and weak; no prostate could be observed; and the genital pore is ventral, at the left of the median line near the level of the posterior margin of the ovary.

At first it seemed possible that the presence of four or five testes represented either a developmental or degenerative phase of the condition in *Spirorchis* and *Henotosoma*, where ten testes are present, and that these small slender forms were young stages of spirorchids. But specimens taken from the vascular system at intervals of a few weeks from the time of capture of the hosts for a period of over a year prevent such a conclusion. The form reaches sexual maturity and continues to live and function without increase in size or in the number of testes.

The ovary is ovoid, lobed, situated on the right side of the body immediately behind the seminal vesicle. The broader end is anterior and pressed against the cecum of the right side, the other end is almost in the median plane. In size the ovary measures from 38 by 48 microns to 46 by 53 microns. The oviduct arises at the posterior end and passes posteriorly on the right side of the body. It has an enlarged portion filled with sperm and then turns toward the median line, where the seminal receptacle branches from the duct. The seminal receptacle narrows to form Laurer's canal, which opens to the dorsal surface near the median line. The common vitelline duct opens into the oötype immediately after the origin of the seminal vesicle and the oötype is followed by the uterus. The vitellaria are well developed and surround the intestinal crura throughout their length, filling the intercrural area anterior to the testes and posterior to the oötype. Median ducts from the lateral masses unite to form the vitelline receptacle that opens into the oötype. Eggs in the uterus measure 54 by 38 microns, a tremendous size for so small a worm. The eggs are oval, golden yellow in color and provided with an operculum.

In general features this genus resembles both *Spirorchis* and *Henotosoma*. It is much smaller and more slender than either and has fewer testes, but the fundamental arrangement of the organ systems is the same. In its slender and elongate form, the location of testes in the posterior half of the body, and in the long interval between the bifurcation of the alimentary tract and the testicular area, it is similar to *Henotosoma*;



but the esophagus is relatively longer and the genital pore farther anteriorly. In the large oral sucker and in the position of the genital pore it resembles certain species of *Spirorchis*, but it differs from *Spirorchis* in number and location of the testes.

Type host: *Chrysemys picta*.

### **Hapalotremineæ** Stunkard, 1921

Hermaphroditic, blood inhabiting distomes. Esophagus often with dilated portion or portions, and surrounded by secretive cells. Ceca end blindly near the posterior end of the body. Excretory vesicle branches behind the posterior testis or testes. Ovary and oötype situated near the middle of the body and between the testes; genital pore dorsal and sinistral near the level of the ovary; vitellaria numerous, both lateral and medial to the ceca throughout most of their course; Laurer's canal present; uterus short containing a single egg which bears either filaments or processes.

The type genus, *Hapalotrema*, contains a single species described by Leared (1862) as *Distoma constrictum* from the heart of the edible turtle, *Thalassochelys corticata*. Monticelli (1896) transferred the species to the genus *Mesogonimus* and gave an extended description of its structure. He featured the developmental stages, eggs, and miracidia, and predicted that *Cercaria dichotoma* is the larval form.

Looss (1899) designated this species as type of a new genus, *Hapalotrema*, and later (1902) added to the description of the form. In this latter paper he suggests that *Hapalotrema* is only one of several species of blood flukes parasitic in sea turtles and he described and figured four different trematode eggs in the blood vessels and tissue in addition to those of *Hapalotrema constrictum*. He was, however, unable to find adults of the other species. From the descriptions of Monticelli and Looss the characters of the genus *Hapalotrema* may be formulated as follows.

Hermaphroditic blood inhabiting distomes; posterior end of body spatulate; anteriorly and ventrally the cuticula bears small spines. Pharynx absent, esophagus similar to that of the schistosomes, ceca end blindly near posterior end of body. Testes both anterior and posterior to the ovary, divided into many (8–10) follicles; seminal vesicle outside of cirrus sac; ovary lobed, on right side near the center of the body; seminal vesicle and Laurer's canal present; vitellaria envelop the ceca throughout their course; uterus short; eggs discharged singly. Genital pore dorsal, on the left side at the level of the ovary. Eggs large, with two long polar filaments which are spirally twisted and thickened at the ends. Present in the heart and arteries of various species of marine turtles.

The writer (1921) included *Hapalotrema* in the family Spirorchidæ and designated it as type of a new subfamily in that group. The next year (1922) I reported the discovery of a second distome from the vascular system of turtles and gave a brief description of the parasite. Its morphological similarity to *Hapalotrema* placed it in the same subfamily,



but differences so marked that they must be considered of generic value prevented its inclusion in the genus *Hapalotrema*. Consequently, a new genus, *Hapalorhynchus*, was formed to contain the species which was named *Hapalorhynchus gracilis*. The discovery of a second genus in the subfamily Hapalotremiæ made it possible to outline the group and formulate the subfamily characters.

The genus *Hapalorhynchus* was characterized by the presence of a protruding oral sucker, acetabulum situated near the posterior end of the anterior third of the body; terminal excretory pore and short median excretory vesicle; testes separated by the ovary; large seminal vesicle and prostate gland anterior to the testes; genital pore dorsal, located near the middle of the body and slightly left of the median line; vitellaria extensively developed in front of the acetabulum and behind the ovary; small seminal receptacle and Laurer's canal; and also by the absence of pharynx, cirrus sac and cirrus.

COMPARISONS.—The genera *Hapalotrema* and *Hapalorhynchus* agree in that both are parasitic in the arterial system of turtles; both are distomes with elongated oval bodies; they agree in the general features of the digestive system; in the lobed form of the ovary and its position between the testes; the extent of the vitellaria; the short form of the uterus; the large size of eggs, which are discharged almost as soon as formed; and in the position of the genital and excretory pores. The two genera differ in many respects and in certain features the disagreement is notable. *Hapalorhynchus* is more slender; the acetabulum is farther posteriad; and the concave spatulate posterior end is lacking. The oral sucker is protrusible; the esophagus is relatively longer; and the ceca do not extend as far posteriad. The greatest differences, however, are found in the reproductive organs. In *Hapalorhynchus* the testes are not divided into separate follicles; the seminal vesicle is anterior to both testes and not between them; a large prostate gland is present; and cirrus sac and cirrus are absent. In this genus, instead of polar filaments, the eggs have three processes, two at one end and one at the other, which gives the egg a tricornuate appearance and probably facilitates its passage through the tissues.

#### ***Hapalorhynchus gracilis* Stunkard, 1922**

Plate XII, Figures 50 to 52; Plate XIII, Figures 53 to 61

This species has been found but once, in the material of *Chelydra serpentina* received November, 1921, from North Judson, Indiana. Of the twelve host specimens, seven were infected with this parasite. Eight



of the twelve turtles have been dissected and furnished the material on which the description of the species was based. Four of them are alive at the time this manuscript is being prepared (September 1922). They have been kept separate in glass aquaria and the feces examined from time to time. Three of the four are infected with *Henotosoma hæmatobium* and many eggs containing living embryos are found in the feces. Two were infected with *Hapalorhynchus gracilis* and, although frequently dark-colored eggs of this form appear in the feces, they are no longer plentiful and do not contain living embryos. These observations would indicate that the adults of *H. gracilis* have died because egg production probably continues throughout the length of life of the parasite; at any rate, I have never seen one in which the ovary was exhausted. *Hapalorhynchus* and *Henotosoma* may both be present in the arteries of the same turtle without apparently affecting each other and it seems that the former is shorter lived. Of course it is impossible to draw conclusions from one or two observations, but the data are worth recording.

Over one hundred specimens of *H. gracilis* were teased from the arteries and collected from the washings of the visceral organs of the five snapping turtles parasitized by this species that have been dissected. Worms were found in the lungs, liver, kidneys, mesenteries, and wall of the alimentary tract. For a short time after they are removed in normal salt solution the worms may show slight movement but I have never witnessed strong or energetic movements and they soon become inactive. The oral sucker is protruded and retracted; the anterior part of the body is extended and contracted; the acetabulum is mobile; but behind the acetabulum the body is less active and often motionless. Living specimens may extend to a length of 2.5 mm. and contract to half this length, the width increasing as the longitudinal muscles contract. The worms (Fig. 50) are fusiform in shape, widest near the center of the body, and taper anteriorly and posteriorly in a similar manner. Before and behind the limits of the vitellaria the body narrows considerably; and cross-sections (Figs. 53, 54) cut at these levels are almost circular. In certain worms (Fig. 54) the body is even compressed laterally at the ends but usually it is slightly flattened dorso-ventrally. The development of the reproductive organs increases its width and cross-sections cut through the middle of the body (Figs. 56–61) are oval, slightly flattened ventrally. Fixed and mounted specimens measure from 1.5 to 1.9 mm. in length, from 0.15 to 0.23 mm. in width, and from 0.092 to 0.12 mm. in thickness.

The cuticula is thin and, unlike that in *Hapalotrema*, is unarmed. The musculature is weak and poorly developed. The suckers are of



moderate size, flexible, but the walls are thin and the muscles not strong. Branching parenchymous fibers pass between the two limiting membranes (Fig. 55). The dermo-muscular sac is exceedingly delicate, weaker even than that of *Spirorchis*, and it is almost impossible to distinguish layers of muscular fibrils. The acetabulum (Figs. 52 and 55) is slightly protrusible but not stalked and is situated near the caudal end of the anterior third of the body. It is cup-shaped, normally circular in outline but sometimes elongated or flattened as a result of pressure or contraction. It measures from 61 to 69 microns in diameter and its depth is approximately equal to its width.

The oral sucker (Fig. 52) is situated at the anterior tip of the body and is capable of considerable extension and retraction. In fixed and mounted specimens, usually about one-half of the sucker protrudes from the body. In shape it is ovate, wider anteriorly, and measures from 0.073 to 0.084 mm. in length and from 0.054 to 0.058 mm. in extreme width. The mouth opening is subterminal (Fig. 52), and the esophagus extends posteriorly from the oral sucker to the bifurcation of the alimentary tract midway between oral and ventral suckers. It is straight in extended specimens, often with two or three dilated portions. The lining is cuticular and it is surrounded by secretive cells. The cells are few in number and do not form an enveloping layer as in *Spirorchis* and *Henotosoma*. Neither do they increase in size and number to constitute the large, deeply staining gland at the posterior end of the esophagus which is so conspicuous in *Spirorchis* and *Henotosoma*. No pharynx is present. The digestive ceca diverge from the esophagus at an angle and end blindly about one-fifth of the body length from the posterior end. They are somewhat dorsal in position (Figs. 55-61) and the left crux is flexed mediad and dorsad near the middle of the body, passing on the median side of the genital pore (Figs. 50 and 59). The intestinal crura are slender, almost straight, and with an almost uniform diameter.

The excretory pore is located at the posterior end of the body, and a large median collecting vesicle (Fig. 50) passes forward, dividing near the caudal limits of the vitellaria to form two lateral collecting ducts. These pass forward on the dorsal side of the body, but whether they continue a dorsal course I am not certain.

The nervous system is not so well developed as in other blood flukes. Even the esophageal commissure is not distinct in whole mounts and the nerves can not be traced in sections without the use of special technique. The esophageal commissure is situated a short distance behind the oral sucker but is much smaller than that of *Hapalotrema* as described and figured by Monticelli.



The testes are situated one behind and the other before the ovary. They are not divided into follicles as in *Hapalotrema* but the organs frequently are faintly lobed. The posterior testis is the larger; it has an elongated oval form and measures 0.18 to 0.21 mm. in length, 0.05 to 0.06 mm. in width, and 0.06 to 0.07 mm. in depth. The anterior testis is situated obliquely, immediately in front and slightly at the right of the ovary. It is ovate to triangular in outline; the widest portion is anterior and median; and the organ narrows laterally and posteriorly. The posterior end occupies the right side of the body at the ovarian level. Its long axis measures from 0.064 to 0.084 mm. and its transverse axis 0.04 to 0.05 mm.

There is a large seminal vesicle (Figs. 50 and 56), which extends from the level of the acetabulum about one-half the distance posteriad to the ovary. On the right side it frequently has one or two indentations and is partially covered by a lobe of the vitellaria. In cross-section it is almost circular and in mature worms is filled with spermatozoa. From the median posterior margin of the vesicle the ejaculatory duct (Figs. 52, 57) emerges as a small tube. It enlarges almost immediately and passes posteriad, dorsad and sinistrad to the genital pore. The anterior part has an epithelial lining and is often filled with spermatozoa, while the terminal part has a cuticular lining and is usually empty. Near the genital pore the duct contracts to a small tube which opens to the dorsal surface just median and anterior to the opening of the uterus. The pore (Fig. 59) is double, the male and female canals opening separately, although the intervening wall is very thin and they appear to discharge through a common orifice. A cirrus sac and cirrus are lacking. The caudal portion of the seminal vesicle and the ejaculatory duct are enclosed in a large, lobed, prostate gland, which occupies most of the body space between the vesicle and the anterior testis.

The female reproductive system is very similar to that of *Hapalotrema*. The ovary in *Hapalorhynchus* is only faintly lobed, while in *Hapalotrema* the indentations are prominent, but otherwise the comparisons are very close. In *Hapalorhynchus* the ovary is ovoid to pyriform in shape, situated obliquely in the body with its long axis almost at right angles to the long axis of the worm. It is slightly at the left of the median line and posterior to the middle of the body. The broader end is anterior and at the left; the smaller end posteriad and right of the median line. Its long axis measures from 0.1 to 0.12 mm. and its shorter axis from 0.06 to 0.08 mm. The oviduct arises at the posterior end and passes posteriad almost to the level of the posterior testis. Here it gives off a seminal



receptacle, often filled with spermatozoa, and Laurer's canal passes dorsally, opening to the surface (Fig. 61) near the median line. Immediately following the seminal receptacle the female duct receives the duct from the vitelline receptacle, and then passes forward on the dorsal side of the body to the genital pore. The vitellaria (Figs. 55-61) consist of masses of follicles extending on either side of the body from the bifurcation of the alimentary tract to the bifurcation of the excretory vesicle. They extend to the median line, forming a continuous mass in front of the acetabulum and behind the ovary, except for a small area where the posterior testis, occupying almost all the space between the dorsal and ventral walls of the body, restricts their presence. Between the acetabulum and the ovary they are limited to narrow tracts at the sides of the body lateral to the intestinal diverticula.

The genital pore (Fig. 59) is dorsal in position, situated near the middle of the body, slightly at the left of the median line. The diverticulum of the intestine and the vitelline duct of that side are bent mediad at the level of the pore and pass median to it. This condition suggests strongly that the genital pore has migrated from a ventro-lateral or lateral to a dorsal position, pushing the intestinal and vitelline structures before it.

The uterus is short and in only two of the many individuals examined has an egg been found in the body. The size of the egg makes it practically certain that not more than a single egg can be present in the uterus at one time. The egg (Fig. 51) is tricornuate; the shell is thick and resistant to pressure, although almost colorless. In the body the egg lies in the uterus with the single horn forward and the forward tip is often bent or slightly coiled. The eggs reach the outside world with the feces of the host and are often present in large numbers. Eggs in the feces measured 0.27 mm. in length, 0.07 mm. in width at the level of the embryo, and 0.2 mm. between the tips of the posterior horns. The miracidium develops slowly and in essential features resembles that of the other blood flukes.

Type host: *Chelydra serpentina*.

Holotype.—No. 125, Dept. Lower Invertebrates, Amer. Mus. Nat. Hist.

#### DISCUSSION

The question of the relationship and systematic position of the blood flukes has been discussed by previous investigators, although only Odhner (1912) has attempted any definite arrangement of the forms. The addition to our knowledge of the data afforded by the recently dis-



covered North American representatives of the group furnishes a firmer and better basis for comparison of these parasites and should contribute materially to the solution of the problem.

The genera *Hapalotrema* and *Bilharziella* were erected by Looss (1899). With the exception of the human forms belonging to the genus *Schistosoma*, they were at that time the only known blood flukes. The fundamental agreement of *Schistosoma* and *Bilharziella* made their close relationship apparent. Although he observed the similarity between *Hapalotrema* and the schistosomes in structure of suckers, dermo-muscular sac, and details of the digestive tract, the important items of difference seemed to preclude a phylogenetic interpretation and Looss concluded that these points of resemblance were merely adaptations produced by existence in a similar and constant environment and by the common food supply. The structures most subject to environmental influences appeared to be the ones involved.

The discovery of the blood flukes of fishes and additional genera of schistosomes extended the field for comparative study and Odhner (1912) advanced the idea that the blood flukes are genetically related. Further evidence for this conclusion was afforded by the discovery of the life cycle of *Sanguinicola* and the results of certain Japanese investigators on the life history of *Schistosoma japonicum*. The group of blood-inhabiting trematodes contains distomes, monostomes, and suckerless forms, but this did not constitute a real difficulty since in his earlier studies on the formulation of a natural system for the digenetic trematodes this author had presented convincing evidence to show that the group of monostomes has no inherent and genetic entity and that the forms included under this heading have descended from different distome families. He contended that these forms manifest merely superficial resemblances and that the absence of an acetabulum, due to the gradual diminution and loss of that organ, is a cenogenetic feature of doubtful taxonomic value. In this paper he erected a new family, Harmostomidæ, with two subfamilies, Harmostominæ and Liolopinæ. In the subfamily Liolopinæ he included the genera *Liolope* Cohn, *Helicotrema* new genus, and *Hapalotrema* Looss. He constructed a type series—*Liolope*, *Hapalotrema*, *Bilharziella*, *Ornithobilharzia*, *Schistosoma*,—and regarded *Hapalotrema* as the important and connecting form in the series. He derived the *Bilharzia* type from *Hapalotrema* and deferred to a later paper a discussion of the relation of the blood parasites of fishes.

Noting marked differences in the character of the digestive, excretory, and reproductive systems, Ward (1921) asserted that the inclusion



of *Hapalotrema* in the family Harmostomidæ and subfamily Liolopinæ was an unnatural arrangement and necessitated a large series of exceptions in the descriptions of those groups which disturb their morphological basis. He removed this genus from the subfamily Liolopinæ and outlined a new family to contain *Hapalotrema* Looss, *Spirorchis* MacCallum, and *Proparorchis*, a new genus formed to contain a blood fluke from North American turtles that had been studied by him. Ward regarded the blood flukes of turtles as certainly related to the schistosomes and relatively closely associated with the fish parasites *Aporocotyle* and *Sanguinicola*.

The writer (1921) made corrections and additions to the description of *Spirorchis* and showed the identity of *Spirorchis* and *Proparorchis*. The name Spirorchidæ was proposed for the family outlined by Ward and two new subfamilies, Spirorchinæ and Hapalotremiæ were erected in the group. Concerning the blood flukes of North American turtles the statement was made that their discovery establishes a firmer basis for the conception of the unity and evolution of the blood-inhabiting trematodes. The Aporocotyliidæ of fishes, the Spirorchidæ of turtles and the Schistosomidæ of birds and mammals were regarded as constituting a well-defined group with inherent natural relationships. The opinion was stated that the Spirorchidæ stand in an intermediate position and that the schistosomes are to be derived through them from the Aporocotyliidæ, rather than from the Harmostomidæ as maintained by Odhner.

The discovery of new genera belonging to each of the subfamilies Spirorchinæ and Hapalotremiæ and their description in the present paper confirms the arrangement and conclusions of the earlier paper. Much of the evidence for a monophyletic origin and genetic relationship of the blood flukes has been presented by Odhner and Ward. The similarity of *Sanguinicola* and *Aporocotyle* was discussed by Odhner (1911) and they were included in the same family by him the following year. In an extended comparison Ward (1921) demonstrated the similarity between *Spirorchis* and *Hapalotrema* and included them in the same family. The family Schistosomidæ manifests so many common and unique features that its unity and validity can not be doubted. The three families then appear well outlined, coherent, and firmly established. Proof of the relationship between the spirorchids and schistosomes has been submitted by both Odhner and Ward. Both subfamilies of the Spirorchidæ have been related to the Schistosomidæ, Odhner demonstrating the similarity between *Hapalotrema* and *Schistosoma* and Ward that of *Spirorchis* and *Schistosoma*. In many respects the schistosomes agree



more closely with *Hapalotrema* than with *Spirorchis* and this appears natural since *Spirorchis* shows closer affinities with the fish parasites. With the establishment of the relationship between the Schistosomidæ and Spirorchidæ, there remains only the consideration of the relation between the latter family and the Aporocotylidæ.

*Spirorchis* and *Aporocotyle* agree in the position of the excretory pore and the general features of the excretory system. They are alike in that the musculature is delicate and an acetabulum is lacking. Both have prominent ventro-lateral nerves. The digestive systems of the two correspond in the absence of a pharynx and the presence of esophageal glands. The relative length of esophagus to ceca and the position of the primary bifurcation of the tract compare closely. The reproductive systems are strikingly similar. The testes are situated in the intercecal area anterior to the ovary and, although in *Aporocotyle* they consist of irregularly massed follicles, in *Sanguinicola* they are arranged in a double linear series. In both *Spirorchis* and *Aporocotyle* the terminal part of the vas deferens is enclosed in a small and poorly developed cirrus sac and the cirrus is eversible. This agreement in character of the copulatory organs is significant. In *Aporocotyle* the genital pore is dorsal, at the left of the median line near the posterior end of the body and, although it is anterior to the ovary in *Aporocotyle*, it is behind the ovary in *Sanguinicola*. In *Spirorchis* the genital pore is sinistral on the ventral side of the body but this disagreement I do not regard as important since in the description of *Hapalorhynchus* the migration of the genital pore from a ventral to dorsal position is explained. Other instances of the same condition are not uncommon. In both genera the ovary is oval, situated on the right side of the body a short distance caudal to the testes. The relations of the oviduct, vitelline duct, and uterus are very similar, although in *Aporocotyle* as in *Schistosoma* the uterus is longer and Laurer's canal is lacking. This latter structure is generally regarded as vestigial and its absence in *Aporocotyle* is not subversive to the thesis. The vitellaria in both genera are similarly situated, enveloping the ceca throughout most of their length, although they extend farther posteriad in *Spirorchis*. The single vitelline duct in *Aporocotyle* is explained by Odhner by the reduction of the duct of the left side.

In the excretory, nervous, muscular, digestive, and reproductive systems there is substantial agreement and, although there are dissimilarities, the long series of structural likenesses constitutes conclusive evidence of more than fortuitous and convergent adaptation. One is



then justified in regarding these forms as closely related and the blood fluke series may be regarded as proceeding from *Sanguinicola* and *Aporocotyle* through *Spirorchis* and *Hapalotrema* to the schistosomes.

Modern classification is based primarily on anatomical characters but the data afforded by the study of the comparative anatomy of the blood flukes does not comprise all the evidence for their common ancestry and genetic relationships. Certain physiological and developmental features point very clearly to the same conclusion. That these forms have been able to enter the vascular system and become adapted to life in the blood stream suggests common fundamental likenesses in structure and physiology that may indicate a common origin and relationship.

Further, it is a significant fact that the most degenerate blood flukes, the suckerless forms with reduced alimentary tract, are found in the oldest and most primitive vertebrates, the fishes; while the most highly specialized blood flukes, the diecious forms, are present in the most recent and highly specialized vertebrates, the birds and mammals. This correlation of the evolution of the parasites with the evolution of their hosts is most suggestive and indicates that the blood flukes are a very old group. While the time of their entry into the vascular system can not be determined with anything like certainty from the evidence at hand, it seems probable that they have long been parasitic in the vertebrates. Either they were parasitic in vertebrates before the division of the vertebrate stem and have remained with their hosts through the transition periods and the evolution of the modern classes of vertebrates or they have changed their primary hosts from one class of vertebrates to another as these developed, a power of adaptation that seems very unlikely.

The genetic interpretation of the morphological similarity of the blood-inhabiting trematodes necessitates an explanation of certain structural differences that are present in the group: the reduction in length of the uterus, the degeneration of Laurer's canal, the migration of the genital pore, and the origin of the diecious condition. A satisfactory explanation is, I believe, possible. Existence in the blood vessels and the constant pressure exerted on the fluke by the elasticity of the walls of these tubes would tend to produce a narrow elongated body and prevent the development of a spacious uterus. This constant pressure, varying in intensity with the pulsations of the heart, would prevent the accumulation of eggs in the body of the parasite and actually force them out of the uterus. Since the eggs are voided in the blood vessels and must pass through the tissues of the host to reach the outside world, a process that requires a long period of time, they must be provided with hard shells



and contain large amounts of food material to supply the embryo during the period of migration. This requires the production of large eggs and the increased size of the egg would act as a potent factor in hastening its discharge from the uterus. Consequently, the uterus has been reduced in length and in certain genera the eggs are deposited almost as soon as they are formed. The absence of Laurer's canal in the Aporocotylidæ and Schistosomidæ does not constitute a serious difficulty. This structure is regarded as vestigial by most students of the Trematoda; and Brandes, Goto, Looss, Odhner, Monticelli and others have cited instances to show its gradual reduction and ultimate disappearance. It is entirely lacking in the Monopisthocotylea and certain families of the Digenea, while in others it is represented by a blind sac opening from the oötype. Its absence in the most degenerate and most highly specialized blood flukes is then not surprising. The migration of the genital pore from a ventral to a dorsal position is not unique in the group of blood flukes. A corresponding dorsal migration of the genital pore is seen in *Axine*, *Microcotyle* and *Octobothrium* and its relations were traced by the writer (1917, p. 15). I have met a similar condition in the subfamily Telorchinæ, where the genital pore of *Protenes* is dorsal. The structural conditions in *Hapalorhynchus* as discussed in the present paper show clearly how such migration of the pore has been effected.

The origin of the diecious condition in the Schistosomidæ and an explanation of its appearance present a more serious problem. It is bound up with the whole question of the origin of sex. According to the observations of Cort (1921, 1921a) and Tanabe and Yokogawa, cited by him, in the schistosomes sex is determined at fertilization and all the individuals produced by parthenogenetic multiplication from a given miracidium are of the same sex. According to Lindner (1914), there are two different kinds of spermatozoa produced in *Schistosoma* and this heterozygous condition of the male he contends is responsible for the sexual differentiation of these diecious trematodes. The maturation processes in hermaphroditic forms are not well known; the observations reported are insufficient and far from conclusive but from the work of Goldschmidt on *Polystoma integerrimum*, *Dicrocoelium lanceolatum* and *Zoogonus mirus*, of von Dingler on *D. lanceolatum*, of A. and K. E. Schreiner, Grégoire and Wassermann on *Z. mirus*, of Schellenberg on *Fasciola hepatica*, and von Kemnitz on *Brachycaelium salamandræ*, it appears that the spermatozoa as well as the eggs are all alike and that every zygote contains complete sets of factors for the production of both male and female gametes. The work on *Schistosoma* indicates that the



males are heretogametic, and, if these observations are correct, the problem narrows to an explanation of this change in maturation.

Considerable light is thrown on the problem by a study of aphids, rotifers, and the smaller Crustacea, where sexual reproduction normally alternates with a series of parthenogenetically produced generations and corresponding differences occur in the maturation phenomena. It is true that in these species the female is heterozygous for sex, producing two kinds of eggs, but here experimental alteration of the sex ratio has shown the effect of environmental factors in determining the kind of eggs produced. In these forms environmental conditions seem to be the determining factors that control the type of gametogenesis and the sex of the ensuing individual. In daphnids Smith (1912) has shown that the type of egg and therefore the type of maturation can be influenced by temperature and food. In a series of papers Whitney (1914, 1916 and others) has discovered that rotifers, if fed on small amounts of a colorless flagellate, *Polytoma*, continue to produce parthenogenetic females, but when fed abundantly on *Euglena* or *Chlamydomonas*, chlorophyll-containing forms that produce oxygen, male-producing females appeared and sexual reproduction occurred. A most interesting and significant observation, and one that may bear directly on the origin of the diecious condition of the blood flukes, was made by Shull and Ladoff (1916) that in the rotifers the production of males is correlated with the supply of oxygen. The direct effect of oxygen was later discredited by Whitney (1919) but it appears certain, however, that these investigators have succeeded in influencing the type of maturation by modification of environmental conditions. By influencing maturation in aphids and phylloxerans, Morgan (1909) and von Baehr (1909) have made important observations on the determination of sex. Similar results were reported by Malsen (1906) for *Dinophilus*. Here it seems that the type of maturation is controlled by the size and organization of the egg. In experiments on moths Seiler has shown that the relative numbers of the two kinds of eggs produced can be influenced by temperature changes at critical stages in the process of maturation.

If the character of the gametes is determined by the type of maturation, and if maturation processes are subject to environmental influences, we have a possible explanation for the origin of the diecious condition in the blood flukes. The schistosomes are the only diecious trematodes known and they are found only in the veins of homothermal vertebrates; consequently, the environmental factors that could have caused the change may be estimated. If, on the advent of vertebrates with a four-



chambered heart, complete separation of arterial and venous circulation and a mechanism for maintaining a constant high temperature, the blood flukes for some reason came to occupy the portal and mesenteric veins they would be located in a medium differing distinctly from their relatives remaining in the arteries of the cold-blooded vertebrates. In this new environmental complex undoubtedly inheres the factor or factors responsible for the development of the diecious state. Temperature alone can not be the determinative factor since birds and mammals are infested by many species of trematodes that retain the hermaphroditic condition. To the question why the blood flukes abandoned the arteries and came to lie in the veins of the higher vertebrates, I have no satisfactory answer. Possibly the oxygen content of the arterial blood in the homothermal vertebrates was too great and they found in the veins about the same amount of oxygen as in the arteries of lower forms. Or it may have been due to food considerations. It is true that the portal and mesenteric veins in these forms (and these are the vessels occupied) contain large amounts of nutrient material received from the small intestine and afford a very rich food supply. But that the amount and character of the food is the decisive factor would, I believe, be difficult to maintain. The blood of the homothermal vertebrates differs from that of cold-blooded forms due to the higher temperature, the increased rate of metabolism, and the greater oxygen content. While other factors may have been operative, it seems probable that the increased oxygen and food supply of the venous blood have been the principal ones concerned with the production of the diecious condition.

Although our knowledge concerning the life histories of the blood infesting trematodes is fragmentary, and for only *Sanguinicola* and the human schistosomes has the complete cycle been demonstrated, considerable evidence to support the hypothesis of genetic relationships among the blood flukes is afforded by developmental data. The miricidia of the various forms are strikingly similar and differ markedly from those of other trematodes. Comparison of the miricidia of *Hapalotrema*, *Spirorchis* and *Schistosoma* as figured by Monticelli, the writer, and Cort will show essential agreement in the structure of these larvæ. The cercariæ so far as known are also very similar and belong to the forked-tailed group. Faust (1919), discussing the group of Furcocercariæ, recognized "a complete series of larval forms from those with a pharyngeal sphincter to the human schistosome cercariæ." Morphological similarity in the larval stages may be considered as of more value in determining relationships than similarity in the adult condition, where parasitic adaptation may have obscured original features.



The cercariæ of all these forms probably penetrate the integument of their hosts. The uniformly general and light infection indicates pretty clearly that the cercariæ are not ingested in mass as would happen if the host ate an infected snail and the cercariæ entered the vascular system from the digestive tract, but that they separately enter the body of the host. A significant observation is that among the blood flukes of turtles the heaviest infections have usually been encountered in the very small turtles. It seems probable that in these young animals the skin is more permeable and not so tough and hard as in older and larger individuals.

If the blood flukes are monophyletic (and present knowledge undoubtedly supports that conclusion), the present system of trematode classification is unnatural, deficient, and defective. Here is a group containing distomes, monostomes and suckerless forms which invalidates the accepted classification of the Digenea. No existing suborder will fairly contain the Aporocotylidæ; the Spirorchinæ would be placed with the monostomes, the Hapalotremiæ with the distomes and the Schistosomidæ, containing forms without suckers and others with one or two suckers, could not be assigned to any suborder as at present characterized. The recognized suborders of the Digenea, Gasterostomata, Monostomata, Amphistomata, Distomata, Holostomata, and possibly also the Aspidocotylea, although only part of these forms are digenetic and *Aspidogaster*, the type genus, is monogenetic, are all based on the character of the adhesive apparatus. As has been argued by many authors and forcefully maintained by Odhner, the adhesive organs of trematodes are adaptive, cenogenetic structures developed with the parasitic habit and consequently of secondary importance in taxonomy. The group of monostomes is rapidly falling apart and increasing knowledge of the digenetic trematodes is certain ultimately to lead to a radical and thorough revision of the classification of these forms. Such a work, however, is outside the scope of the present paper.



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## EXPLANATION OF PLATES

All figures except those of reconstructions were drawn with the aid of a camera lucida and, with the exception of those of eggs and embryos, were made from permanent mounts.

## Abbreviations used in Plates II to XIII

|                              |                                |
|------------------------------|--------------------------------|
| AD, anterior duct.           | NM, rudimentary nerve mass.    |
| AP, anterior papilla.        | OC, eye spot.                  |
| CG, cephalic gland.          | OD, oviduct.                   |
| CS, cirrus sac.              | OO, egg.                       |
| ED, excretory duct.          | OS, oral sucker.               |
| EE, esophageal evaginations. | OV, ovary.                     |
| EG, esophageal glands.       | PR, prostate gland.            |
| FJ, ejaculatory duct.        | PV, posterior ventralis nerve. |
| EP, excretory pore.          | RD, rudimentary digestive sac. |
| ES, esophagus.               | SV, seminal vesicle.           |
| EV, excretory vesicle.       | UT, uterus.                    |
| FC, flame cell.              | TS, testis.                    |
| GC, germ cell.               | VD, vas deferens.              |
| GP, genital pore.            | VL, vitelline duct.            |
| IN, intestine.               | VR, vitelline receptacle.      |
| LC, Laurer's canal.          | VS, acetabulum.                |
| MT, metraterm.               | VT, vitellaria.                |
| NC, nerve commissure.        |                                |



PLATE II

- Fig. 1. *Spirorchis innominata*, from whole mount, ventral view,  $\times 27$ .  
Fig. 2. *Spirorchis elegans*, from whole mount, ventral view,  $\times 65$ .  
Fig. 3. *Spirorchis elegans*, from whole mount, much flattened, ventral view,  
 $\times 65$ .



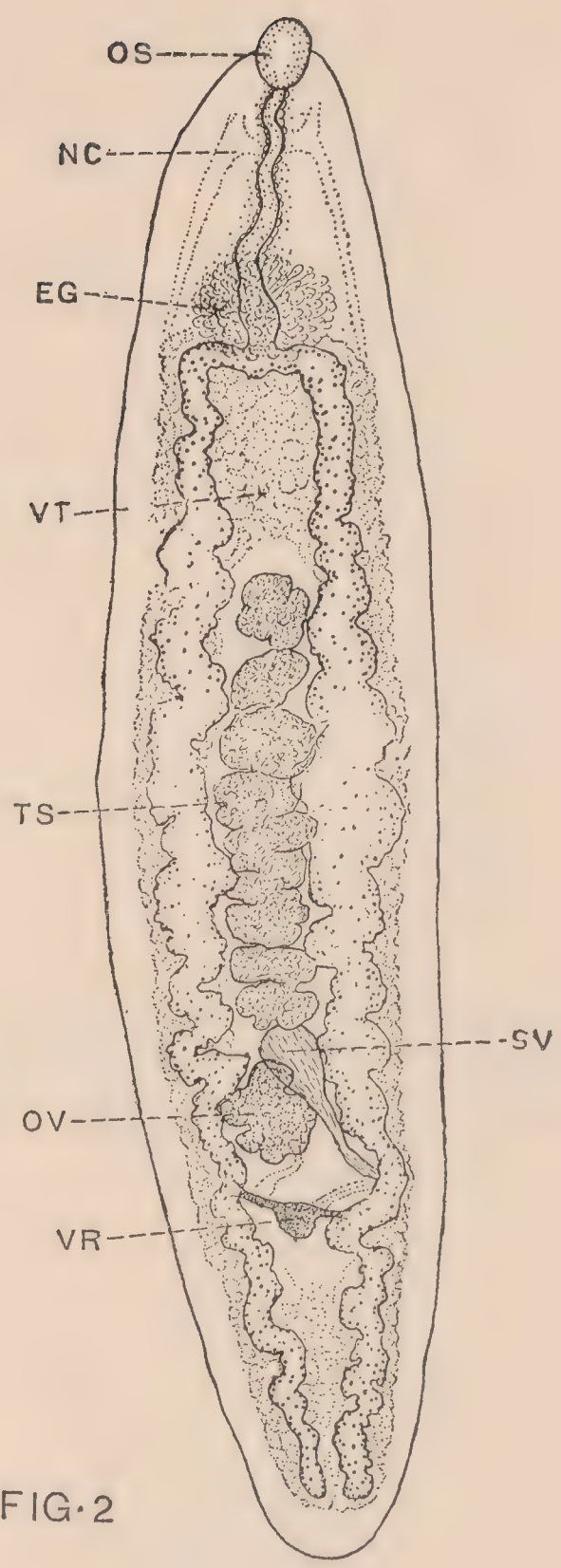
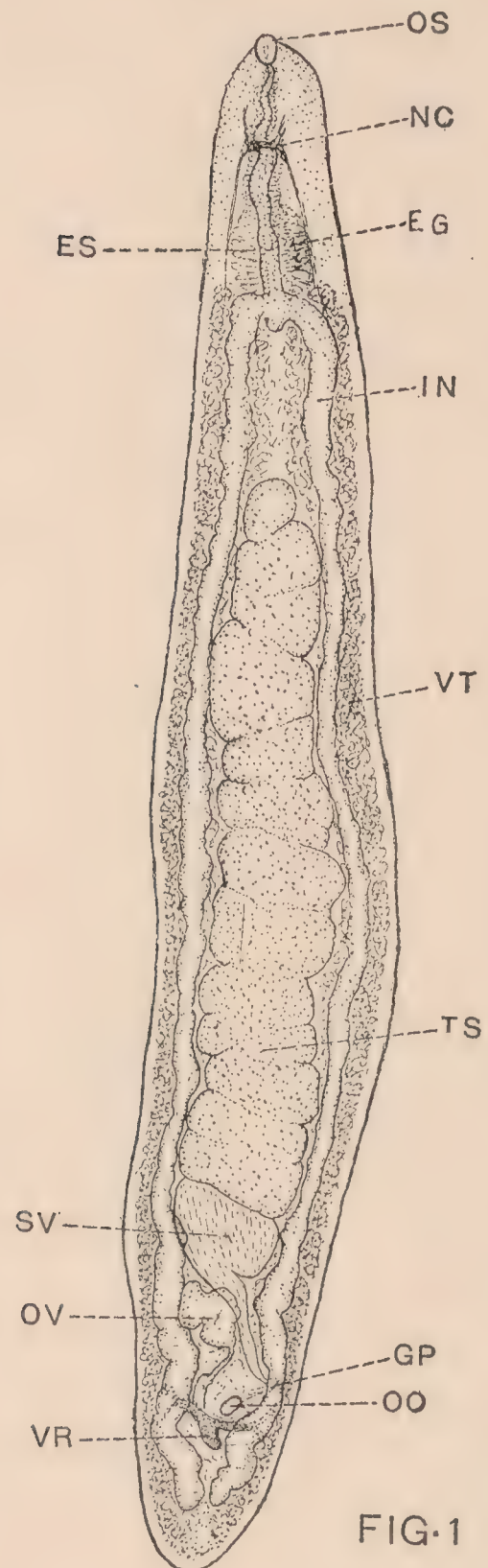




PLATE III

- Fig. 4. *Spirorchis scripta*, from whole mount, dorsal view,  $\times 65$ .  
Fig. 5. *Spirorchis scripta*, from whole mount, dorsal view,  $\times 65$ .  
Fig. 6. *Spirorchis picta*, from whole mount, ventral view,  $\times 65$ .



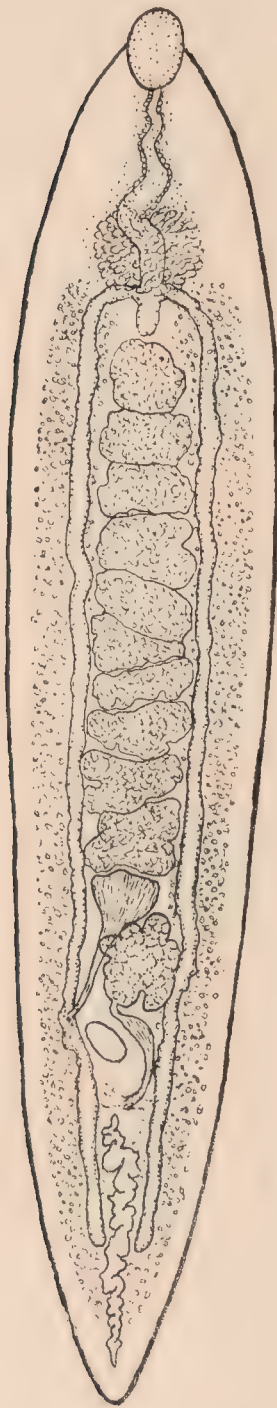


FIG. 4

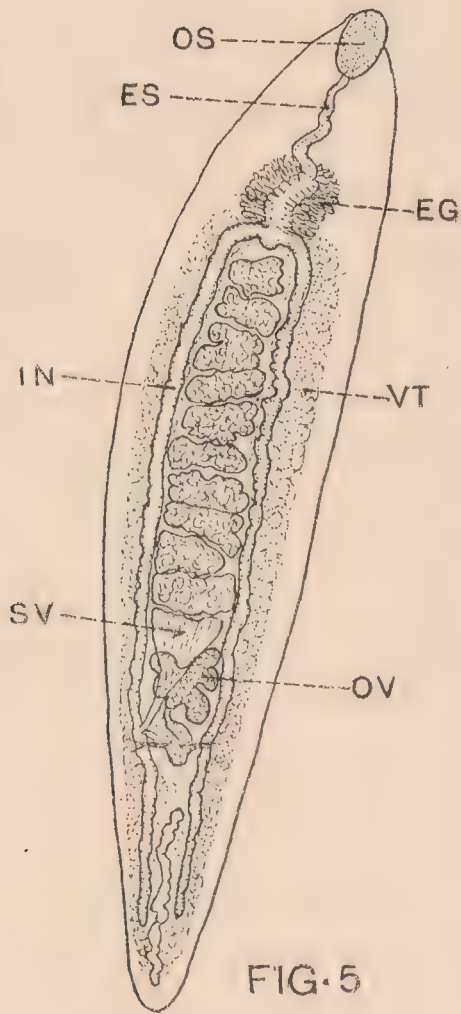


FIG. 5

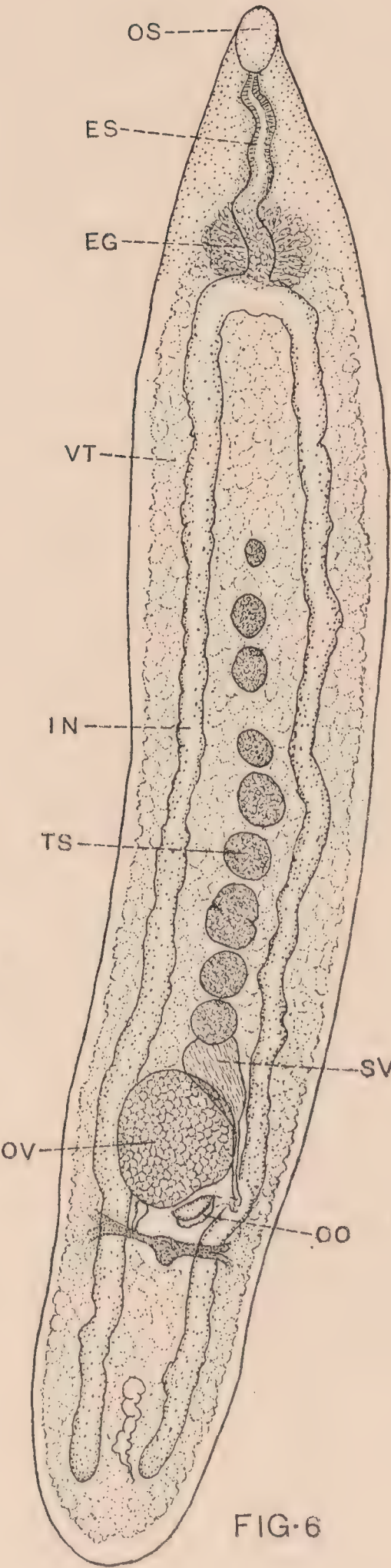


FIG. 6



PLATE IV

*Spirorchis artericola.*

Fig. 7. Specimen from mesenteric arteries of *Chrysemys picta*, whole mount, ventral view,  $\times 65$ .

Fig. 8. Specimen from the mesenteric arteries of *Pseudemys scripta*, whole mount,  $\times 65$ .



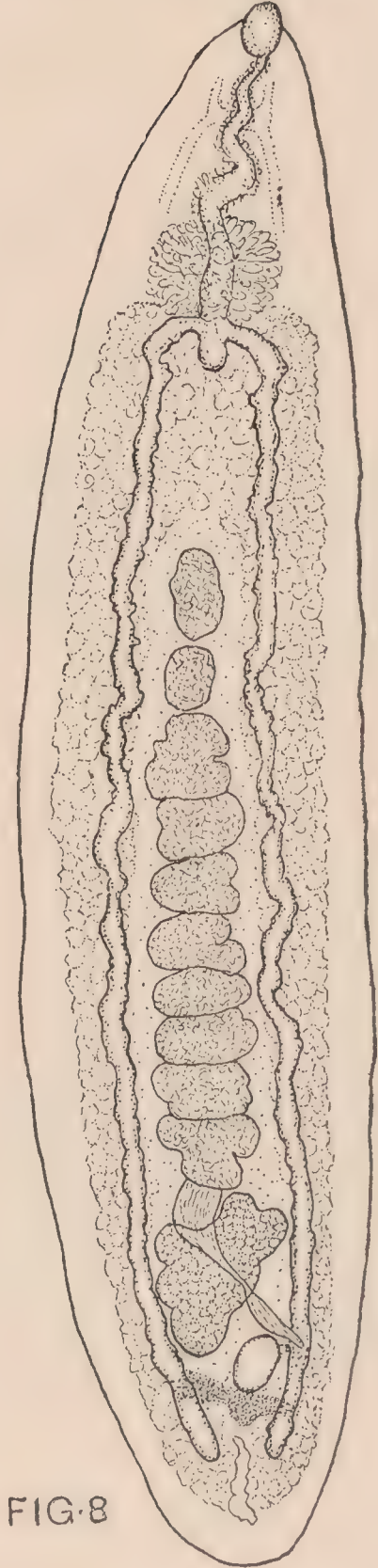
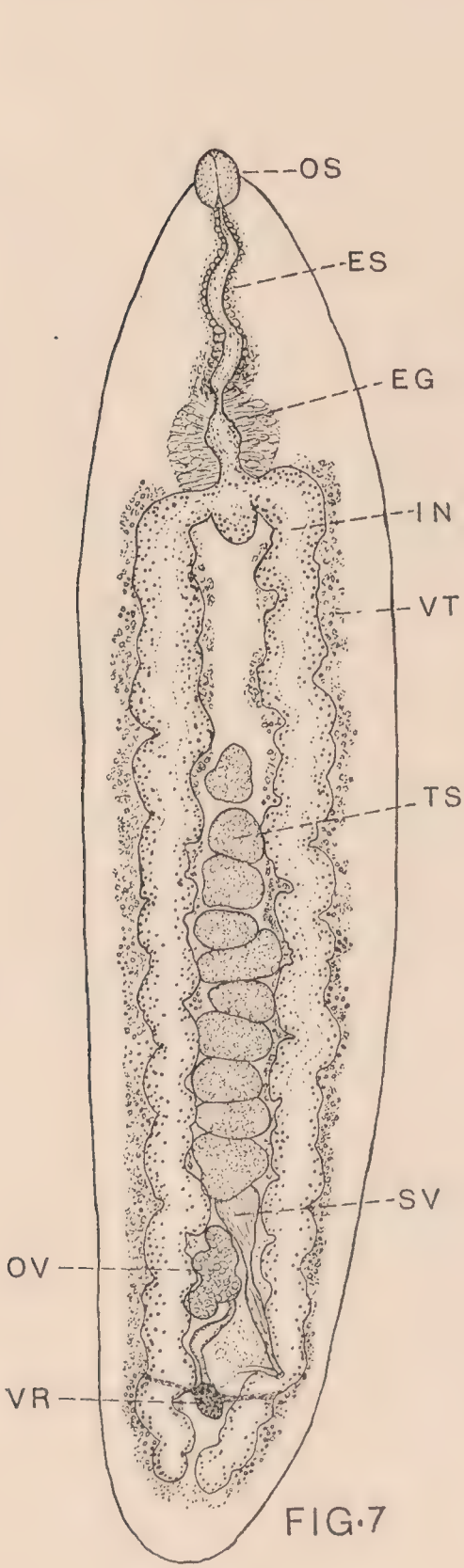




PLATE V

*Spirorchis artericola*.

Fig. 9. Frontal section near the ventral side of the body showing the posterior ventralis nerves, intestinal crura, testes, seminal vesicle, cirrus sac and ovary,  $\times 60$ .

Fig. 10. Sagittal section of the body through the genital pore showing the posterior testis, seminal vesicle, cirrus sac, ovary, uterus, vitellaria and intestine,  $\times 235$ .

Fig. 11. Reconstruction of the posterior end of the body from frontal sections, showing Laurer's canal, the tips of the intestinal crura, the vesicular structure present in this region, the excretory ducts and pore,  $\times 90$ .

Fig. 12. Cross-section of the body immediately anterior to the genital pore, showing sections of the vitellaria, one excretory duct, intestinal crura, oviduct, uterus, metraterm and cirrus sac. The section is cut through a coil of the ejaculatory duct and it appears twice in the figure,  $\times 145$ .



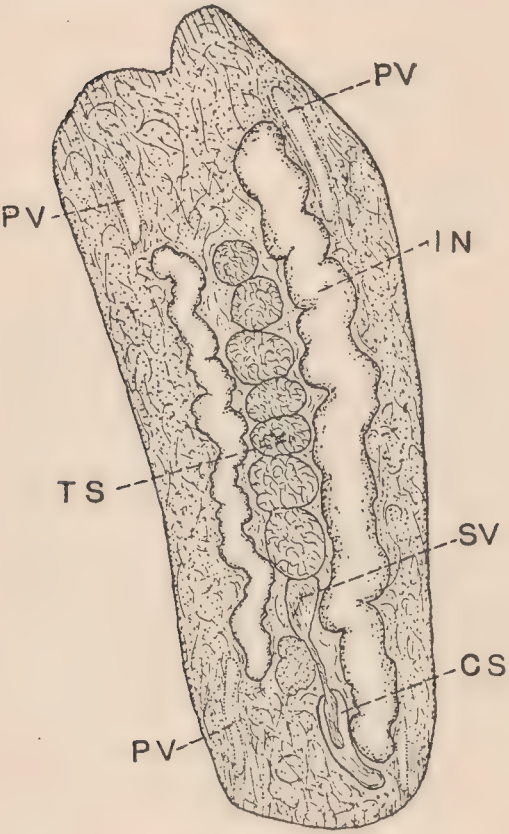


FIG. 9

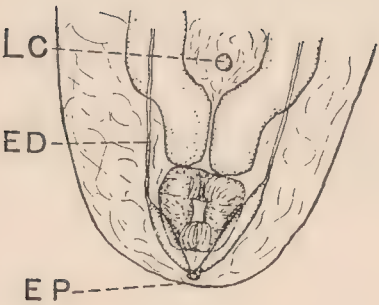


FIG. 11

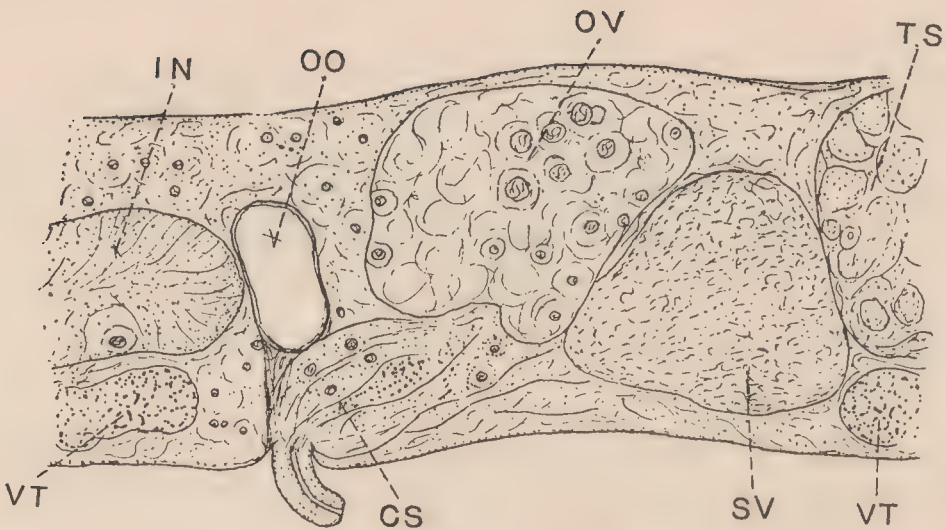


FIG. 10

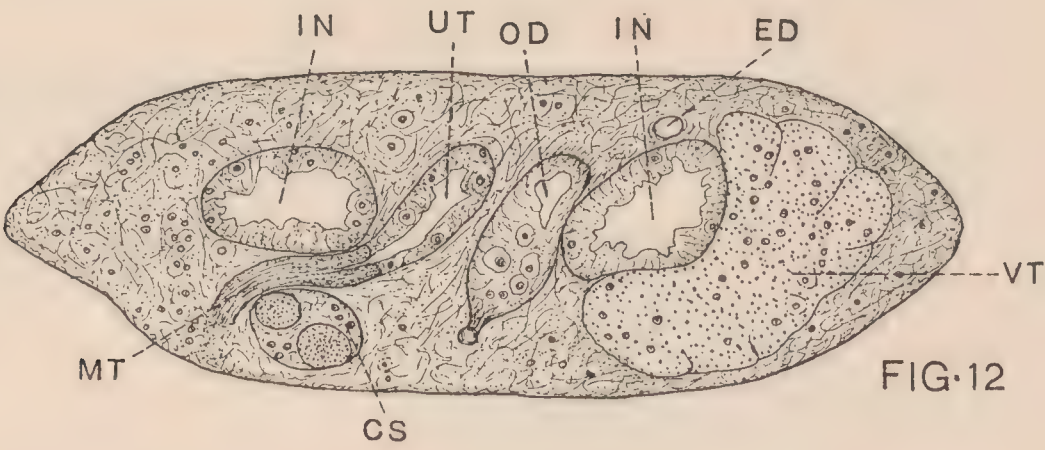


FIG. 12



## PLATE VI

All figures are cross-sections of *Spirorchis artericola*.

Fig. 13. Section through the oral sucker,  $\times 145$ .

Fig. 14. Same specimen as Fig. 13; section through the esophageal commissure of the nervous system and showing also the esophageal evaginations and gland cells,  $\times 145$ .

Fig. 15. Section through another specimen showing the same features as the previous figure. The esophageal evaginations are not so numerous,  $\times 145$ .

Fig. 16. Same specimen as Fig. 15; section immediately anterior to the bifurcation of the alimentary tract, showing the esophageal evaginations and glands, and sections of the anterior lobes of the vitellaria and posterior ventralis nerves,  $\times 145$ .

Fig. 17. Section of another specimen, cut through the bifurcation of the alimentary tract and showing the median posterior ventral pocket,  $\times 145$ .

Fig. 18. Section of another specimen cut through the posterior testis showing testis, intestinal diverticula, excretory ducts and vitellaria,  $\times 105$ .

Fig. 19. Same specimen as Fig. 17; section through the opening of Laurer's canal,  $\times 145$ .

Fig. 20. Same worm as Fig. 16; section behind the intestinal crura, showing the excretory ducts, vitellaria and the peculiar vesicular structure of this region,  $\times 145$ .

Fig. 21. Same specimen as Fig. 20; section through the excretory pore,  $\times 145$ .



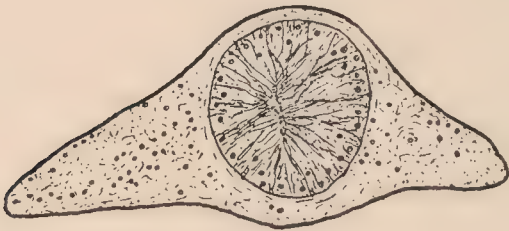


FIG. 13



FIG. 14

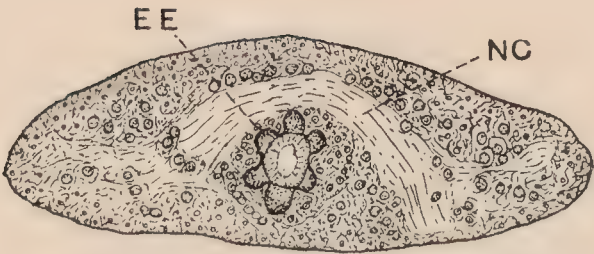


FIG. 15

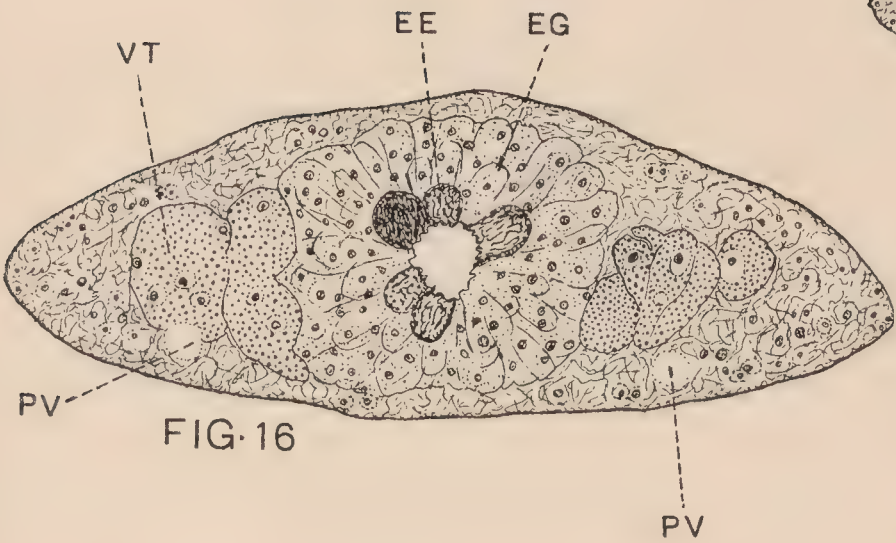


FIG. 16

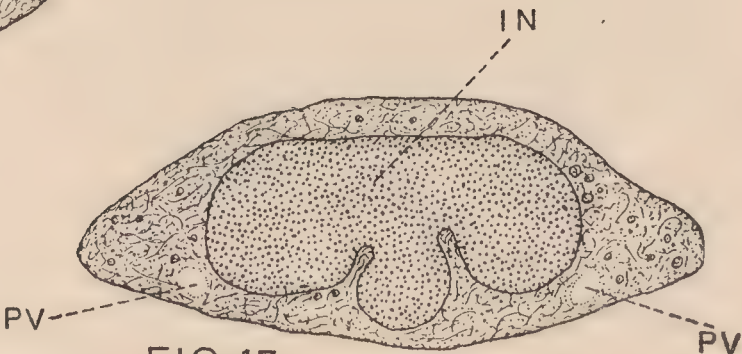


FIG. 17

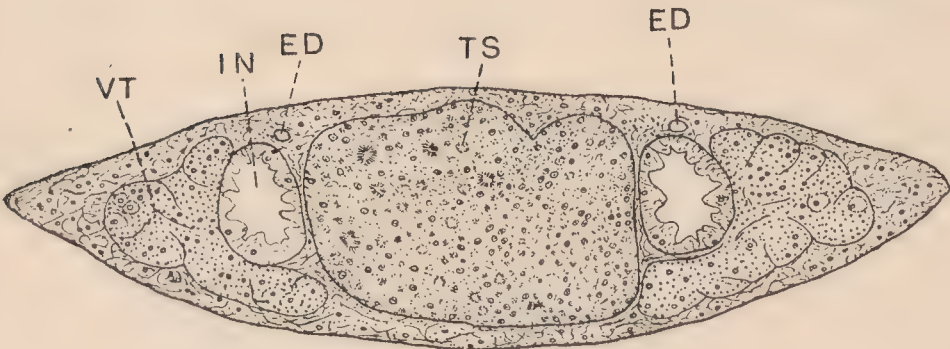


FIG. 18

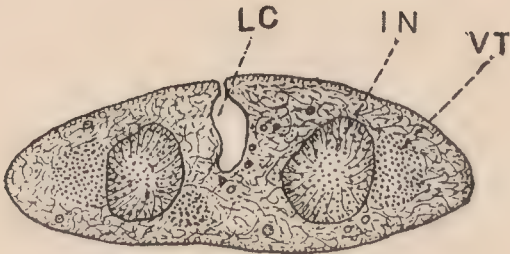


FIG. 19

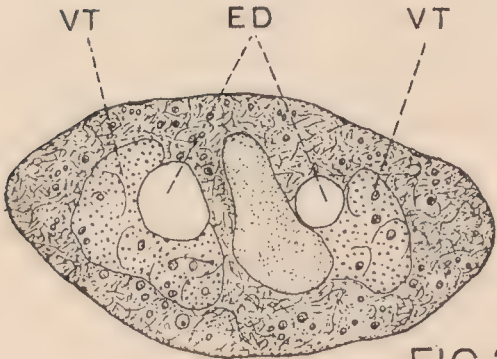


FIG. 20

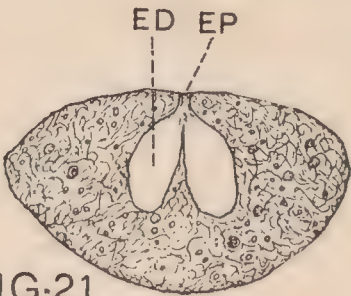


FIG. 21



## PLATE VII

These figures are cross-sections of a mesenteric artery of *Chrysemys picta* containing two specimens of *Spirorchis artericola*. The two worms lie with their anterior ends in the same direction with dorsal sides contiguous, and the figures show cuts at successive levels. Only the media and intima of the artery are reproduced. All are drawn at the same magnification,  $\times 105$ .

Fig. 22. The worm at the top of the figure is cut through the oral sucker and the one below just in front of the anterior testis.

Fig. 23. The worm in the upper part of the figure is cut through the esophageal gland, the one below through one of the testes.

Fig. 24. The specimen in the upper part of the figure is cut through one of the testes, the one below through the anterior part of the ovary and the posterior part of the seminal vesicle.

Fig. 25. The upper specimen is cut through the testis behind the one shown in Fig. 24, and the lower specimen is cut through the posterior part of the ovary and the cirrus sac.

Fig. 26. The specimen in the lower part of the figure is cut through the genital pore, this section showing that these worms did not lie with the genital pores opposed.



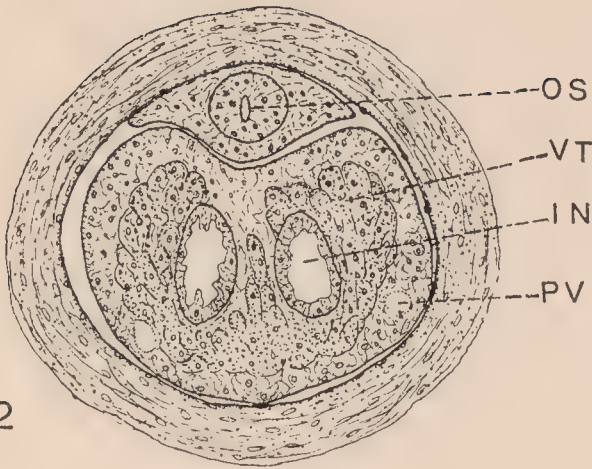


FIG. 22

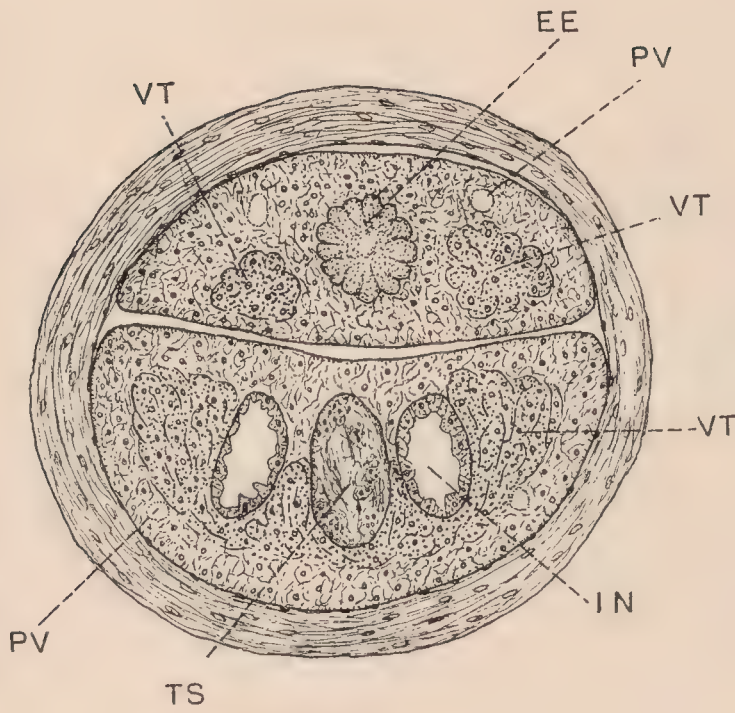


FIG. 23

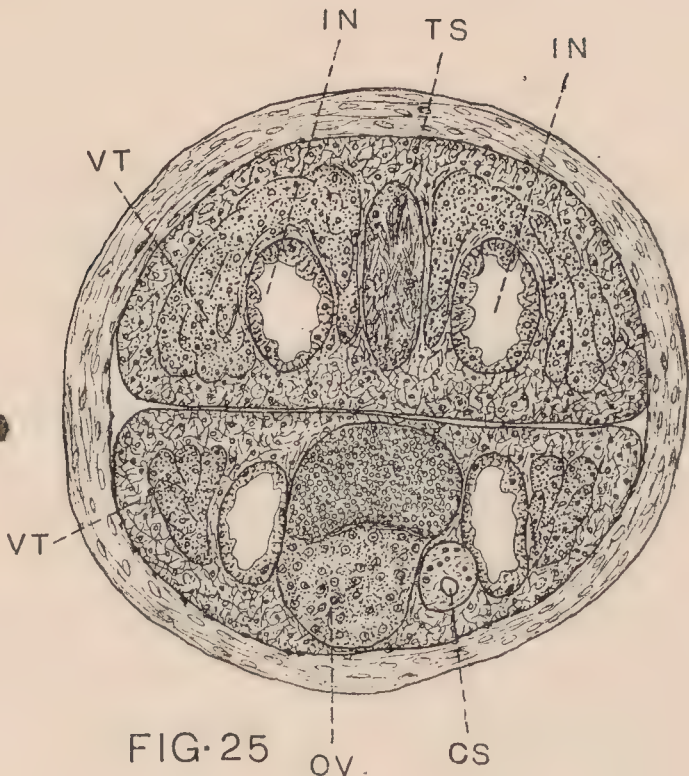


FIG. 25

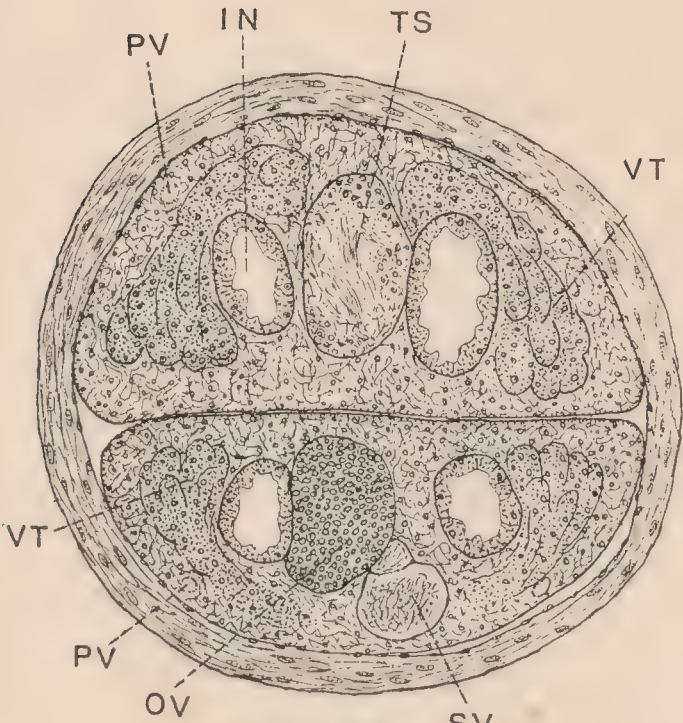


FIG. 24

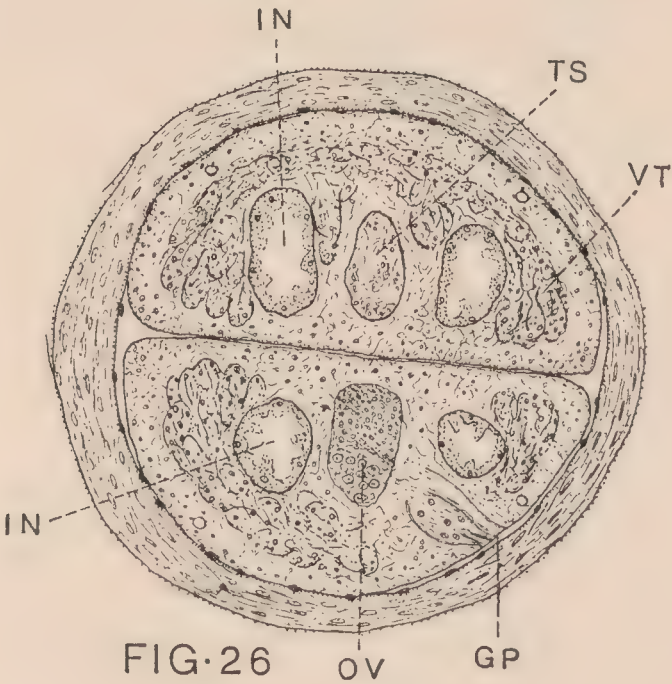


FIG. 26



### PLATE VIII

Series of figures showing developmental stages of *Spirorchis artericola* and structure of the miracidium.

- Fig. 27. Egg just voided from the uterus.
- Fig. 28. Slightly older egg, showing early embryo.
- Fig. 29. Egg containing slightly older embryo with developing eye spots.
- Fig. 30. Egg containing older embryo, cilia developing and three constrictions in the circular muscles of the body.
- Fig. 31. Egg with embryo almost ready to hatch.
- Fig. 32. Egg with operculum just opening.
- Fig. 33. Egg shown in Fig. 32 after emergence of embryo.
- Fig. 34. Embryo from egg shown in Fig. 33.
- Fig. 35. Miracidium, view from the neural surface showing anterior papilla, cephalic glands, rudimentary digestive sac, anterior ducts, eye spots, flame cells, rudimentary nervous mass and germ cells.
- Fig. 36. Miracidium, side view, showing same structures as the previous figure.



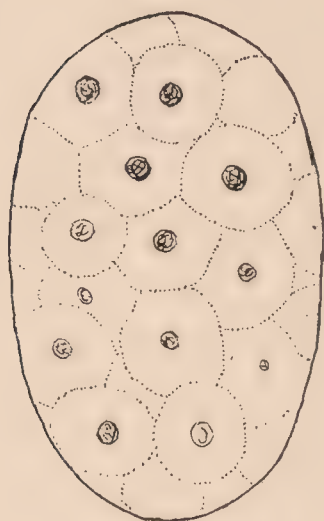


FIG. 27

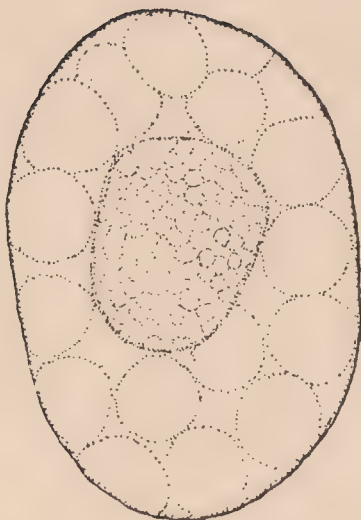


FIG. 28



FIG. 29



FIG. 30

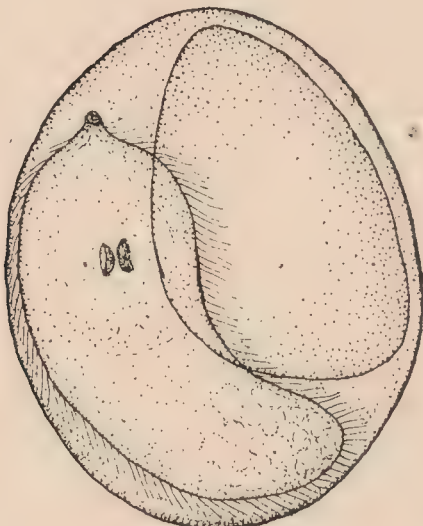


FIG. 31

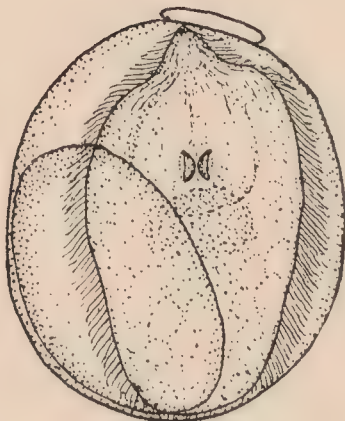


FIG. 32

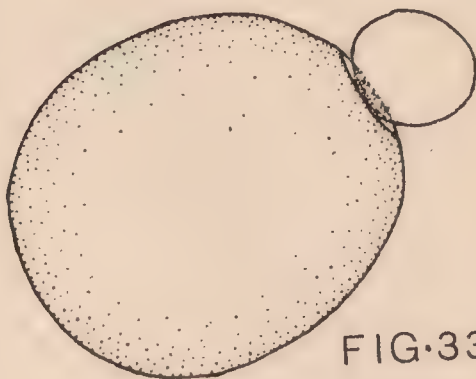


FIG. 33

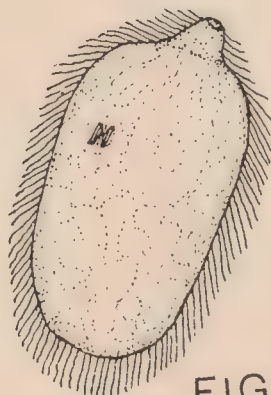


FIG. 34

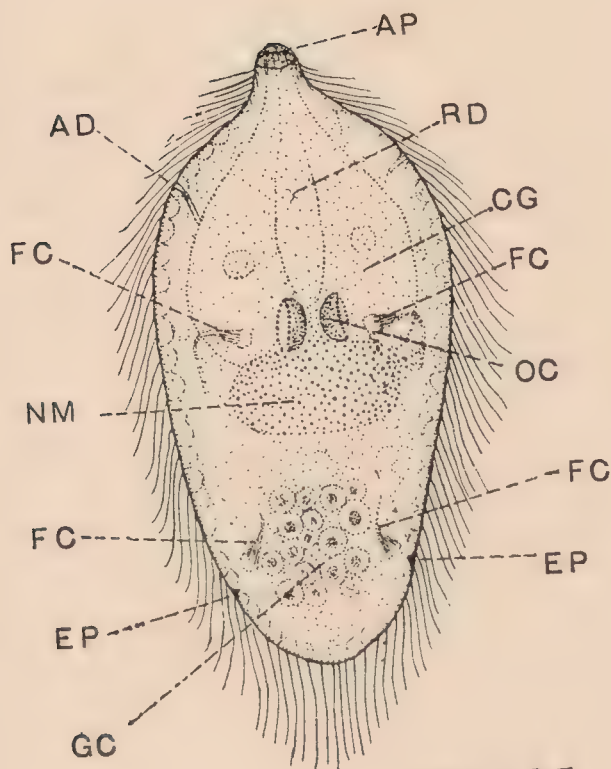


FIG. 35

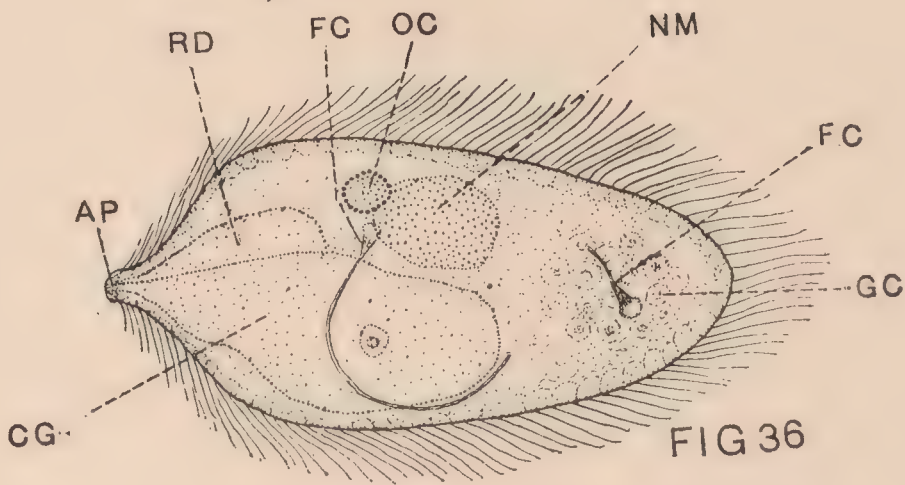


FIG. 36



PLATE IX

Fig. 37. *Henotosoma hæmatobium*, from whole mount, ventral view,  $\times 19$ .

Fig. 38. *H. hæmatobium*, dorsal view, from whole mount, showing the disintegration of the testes. The black object just anterior to the vitelline duct and at the left and behind the ovary is an egg,  $\times 14$ .



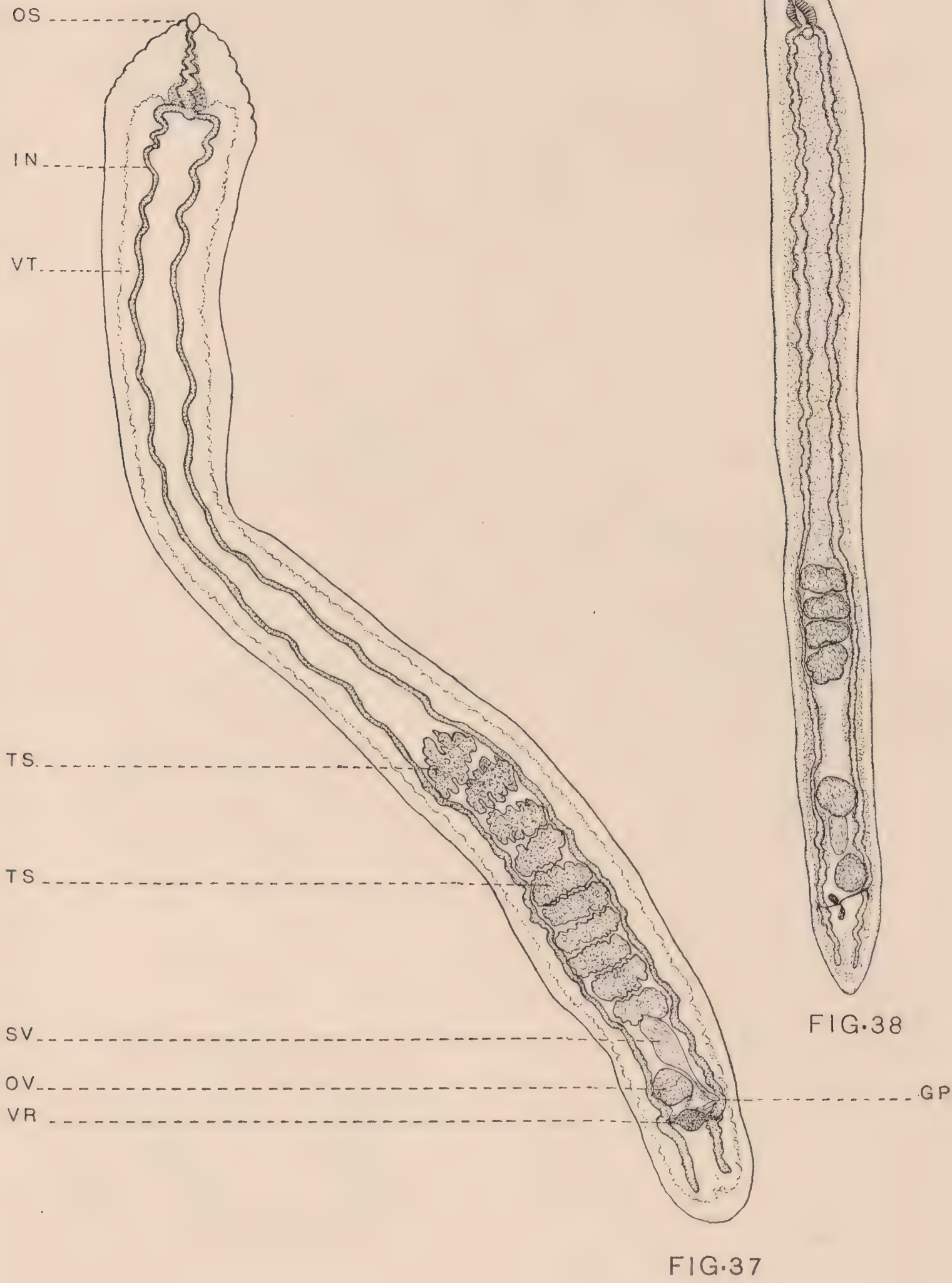




PLATE X

*Henotosoma hæmatobium.*

- Fig. 39. Cross-section through the esophageal gland,  $\times 65$ .  
Fig. 40. Cross-section of body anterior to the testes,  $\times 65$ .  
Fig. 41. Cross-section through one of the testes,  $\times 65$ .  
Fig. 42. Cross-section through the genital pore showing the cirrus extruded,  
 $\times 65$ .  
Fig. 43. Cross-section through the opening of Laurer's canal,  $\times 65$ .  
Fig. 44. Longitudinal section of the posterior part of the worm showing seminal vesicle, cirrus sac, ovary, oviduct, origin of Laurer's canal, uterus, intestine, posterior vesicle and excretory pore,  $\times 62$ .



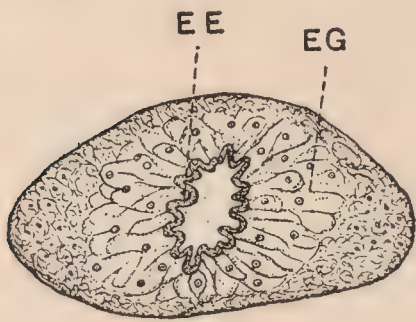


FIG. 39

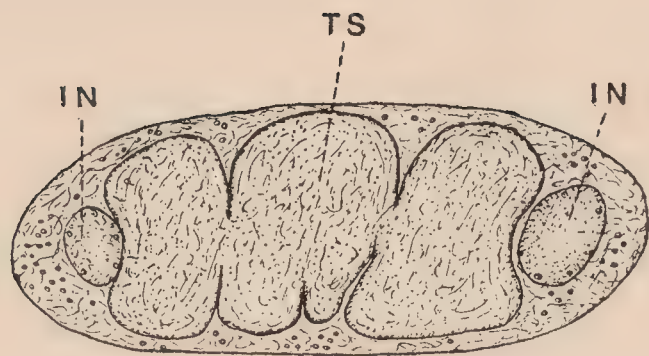


FIG. 41

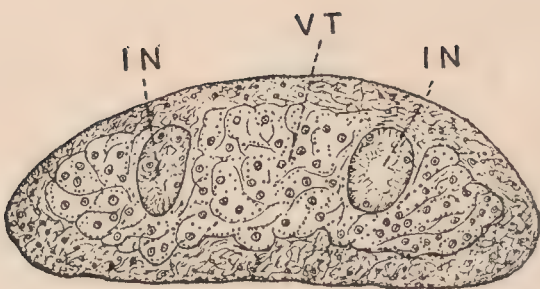


FIG. 40

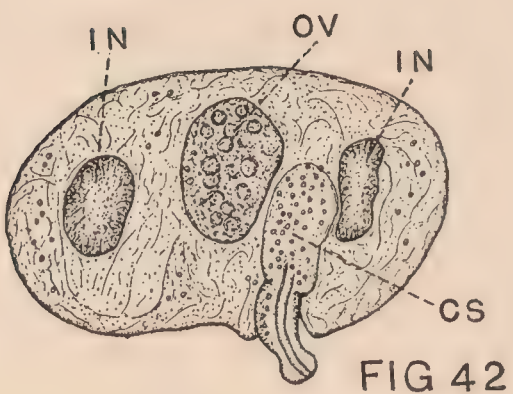


FIG. 42

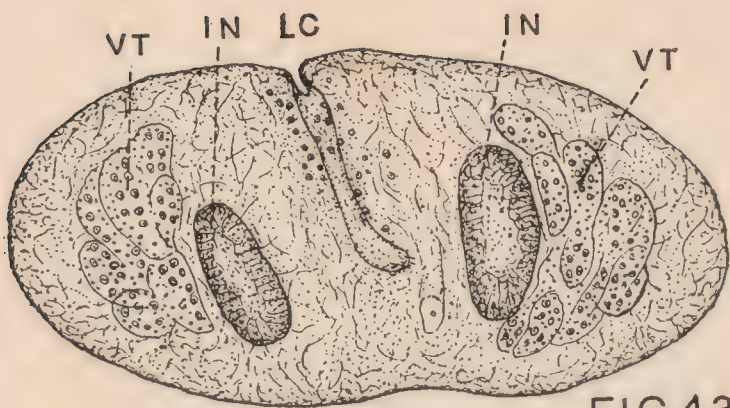


FIG. 43

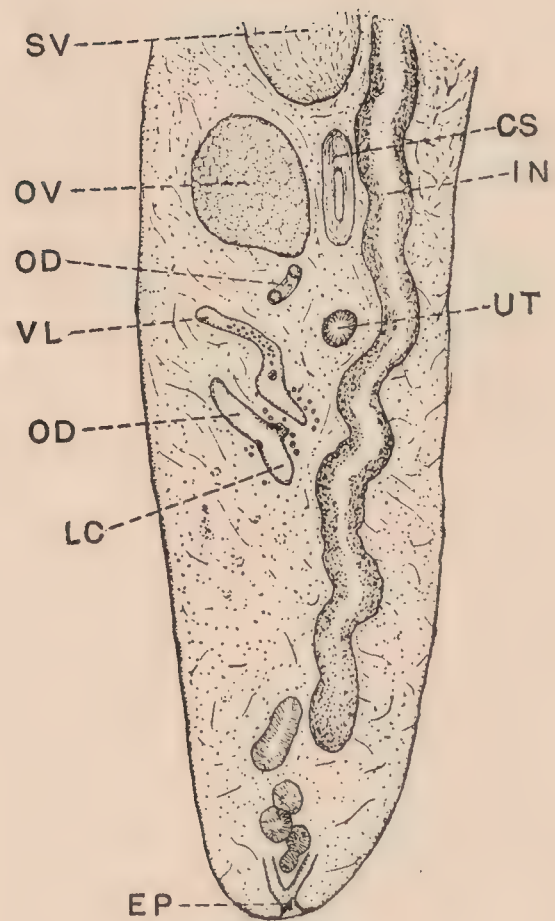


FIG. 44



PLATE XI

*Hæmatotrema parvum.*

Fig. 45. Whole mount, ventral view,  $\times 65$ .

Fig. 46. Sagittal section through the oral sucker,  $\times 105$ .

Fig. 47. Frontal section through the middle of the body showing the bifurcation of the alimentary tract, the testes, seminal vesicle and ovary,  $\times 145$ .

Fig. 48. Reconstruction of the reproductive organs near the genital pore, showing seminal vesicle, cirrus sac, ovary, oviduct, vitelline ducts and receptacle, Laurer's canal, uterus and genital pore,  $\times 260$ .

Fig. 49. Whole mount, dorsal view,  $\times 105$ .



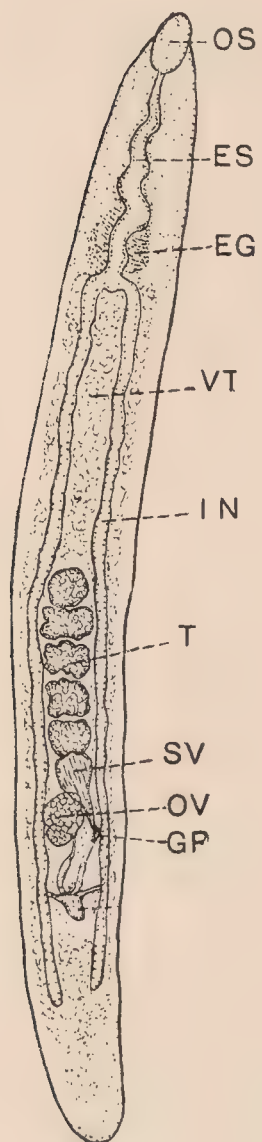


FIG. 45



FIG. 46

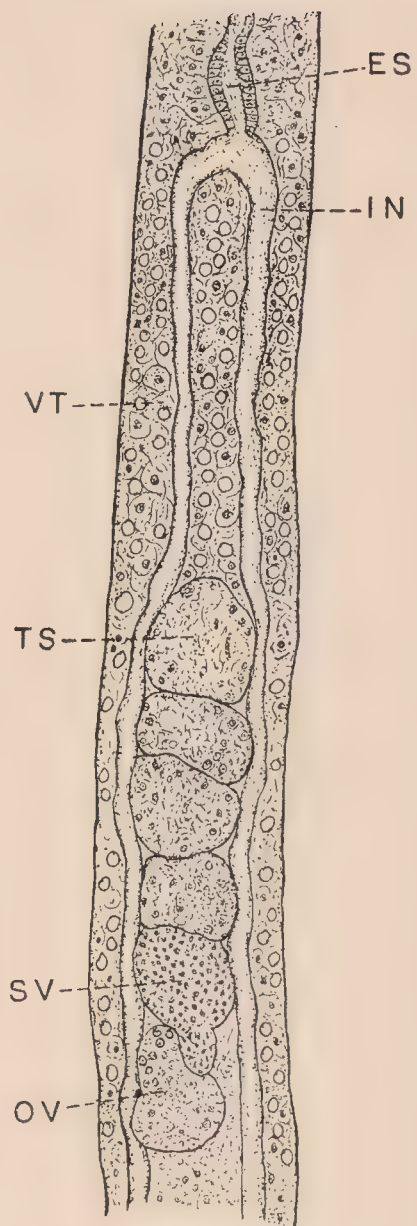


FIG. 47

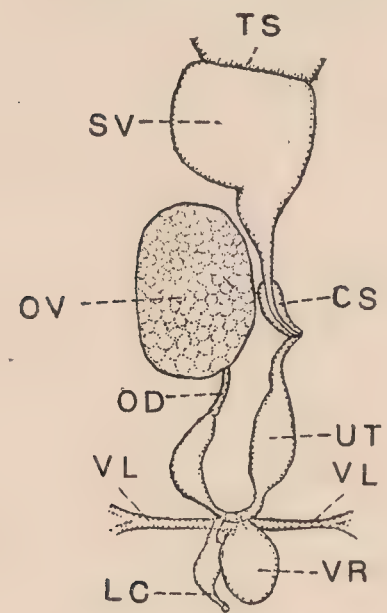


FIG. 48

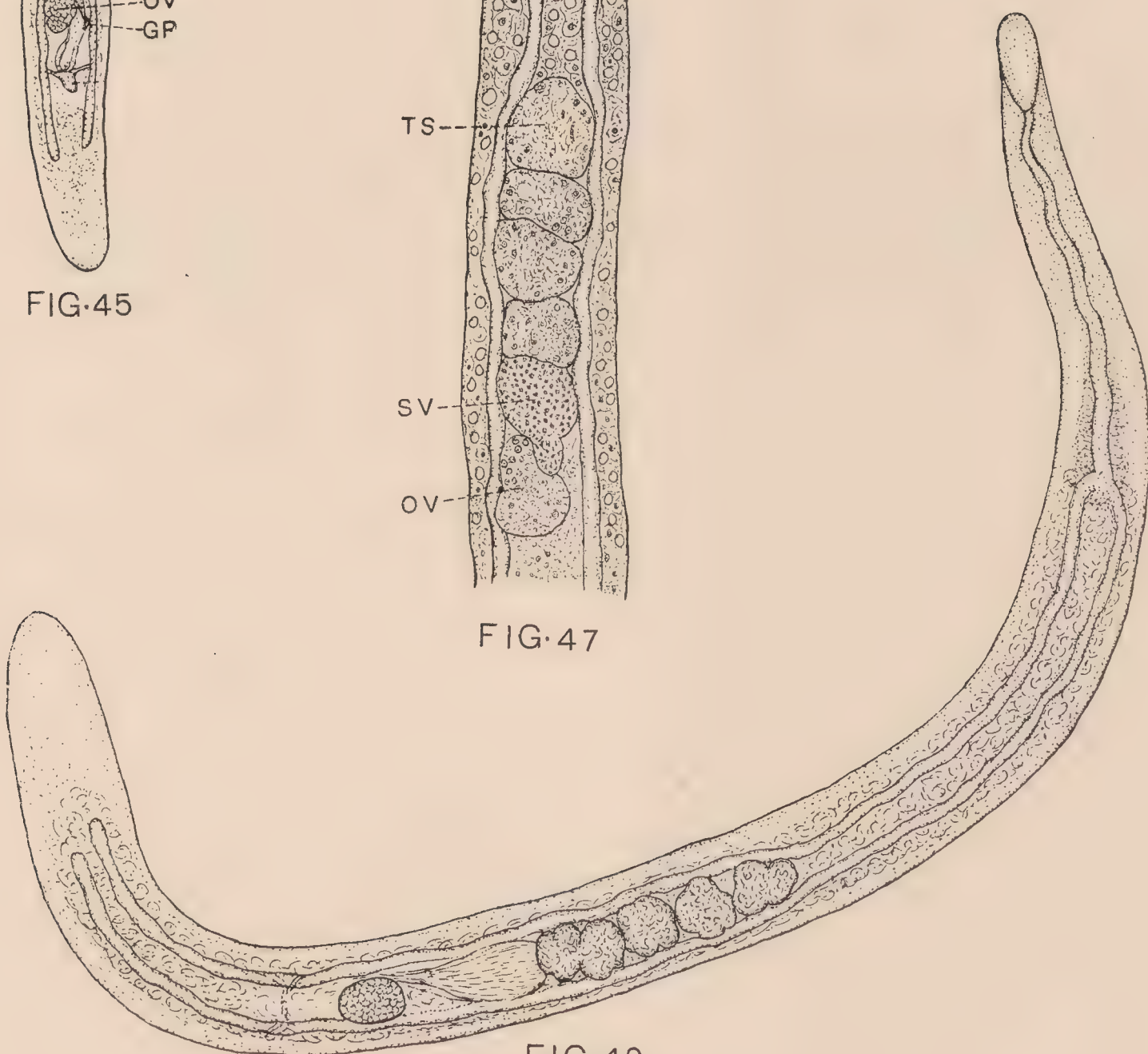


FIG. 49



PLATE XII

*Hapalorhynchus gracilis.*

Fig. 50. Whole mount, dorsal view,  $\times 60$ .

Fig. 51. Egg from the feces of *Chelydra serpentina*,  $\times 125$ .

Fig. 52. Sagittal section near the midline of the body, showing oral sucker, esophagus, intestine, acetabulum, seminal vesicle, origin of the ejaculatory duct, prostate gland, anterior and posterior testes, uterus and vitellaria,  $\times 60$ .



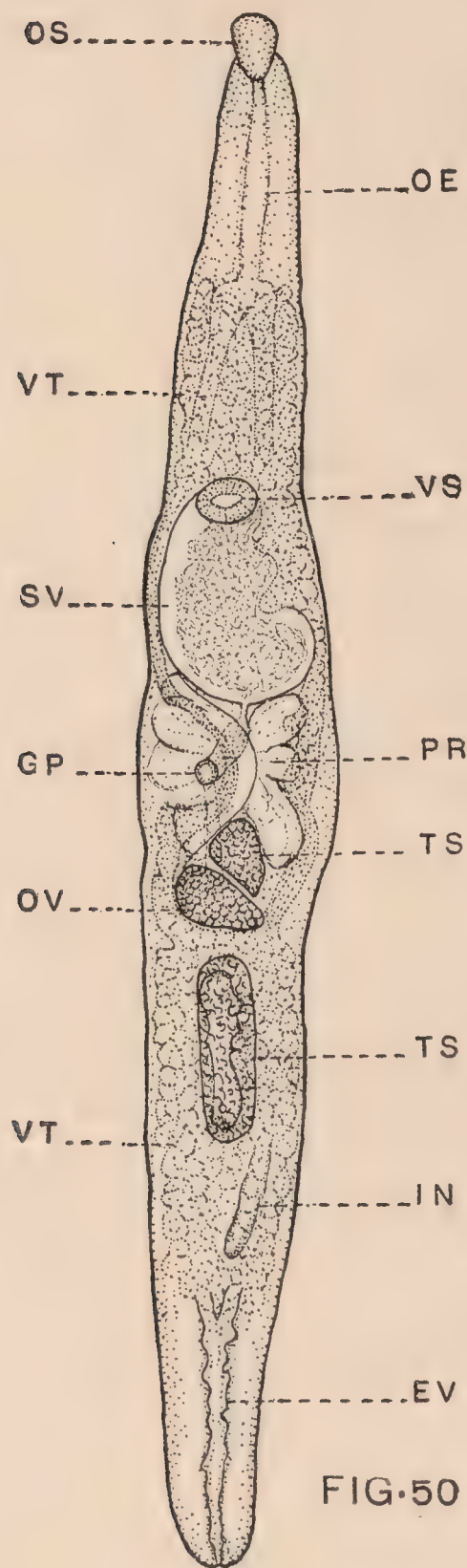


FIG. 50

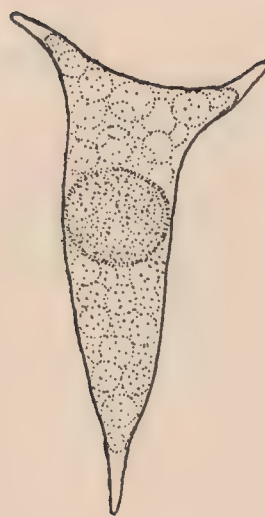


FIG. 51

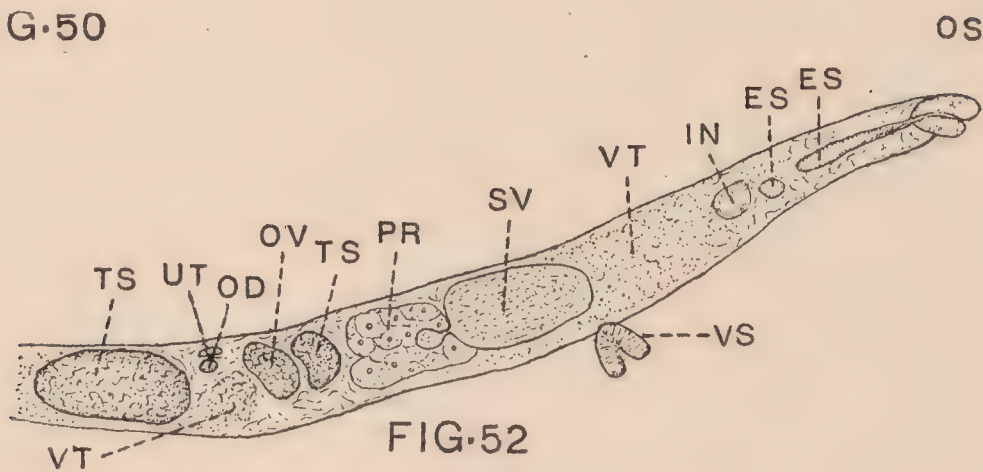


FIG. 52



PLATE XIII

*Hapalorhynchus gracilis*, cross-sections from several specimens but all drawn at the same magnification,  $\times 235$ .

Fig. 53. Section through the esophageal commissure.

Fig. 54. Section at the level of the bifurcation of the alimentary tract.

Fig. 55. Section through the acetabulum showing the relation of structures at that level.

Fig. 56. Section at the level of the seminal vesicle.

Fig. 57. Section cut through the prostate gland near the seminal vesicle.

Fig. 58. Section just anterior to the genital pore, showing the cuticular lining and enlarged portion of the ejaculatory duct.

Fig. 59. Section through the genital pore. Note that the intestinal diverticulum of the left side is dorsal in position and median to the pore.

Fig. 60. Section through the posterior part of the cephalic testis and the anterior part of the ovary.

Fig. 61. Section through the opening of Laurer's canal.



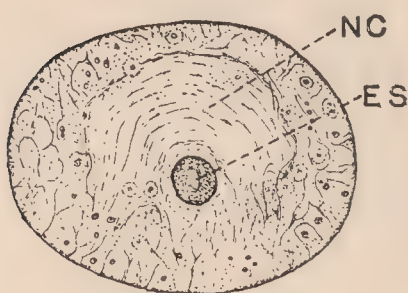


FIG. 53



FIG. 54

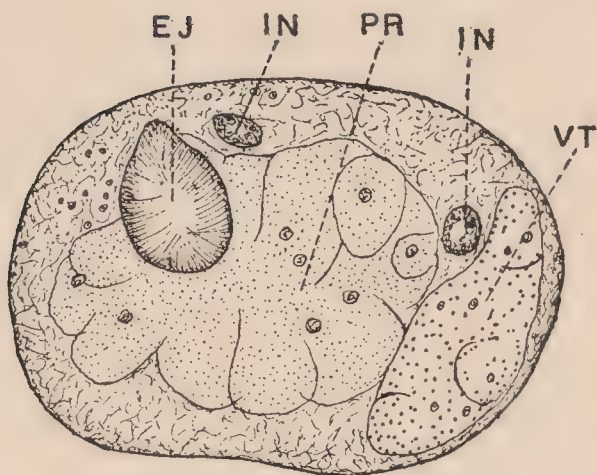


FIG. 58

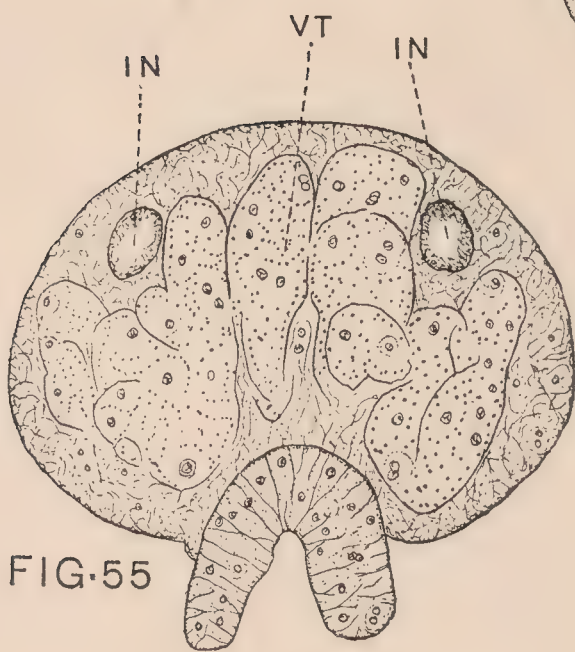


FIG. 55

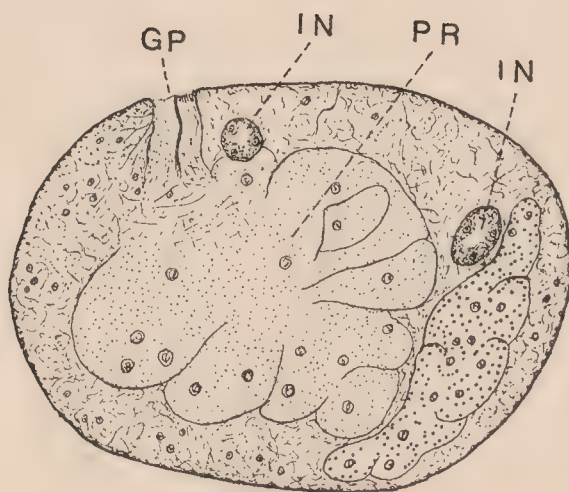


FIG. 59

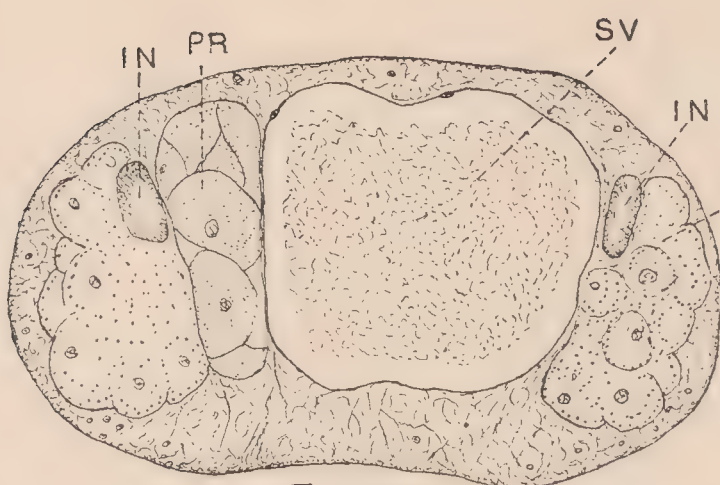


FIG. 56

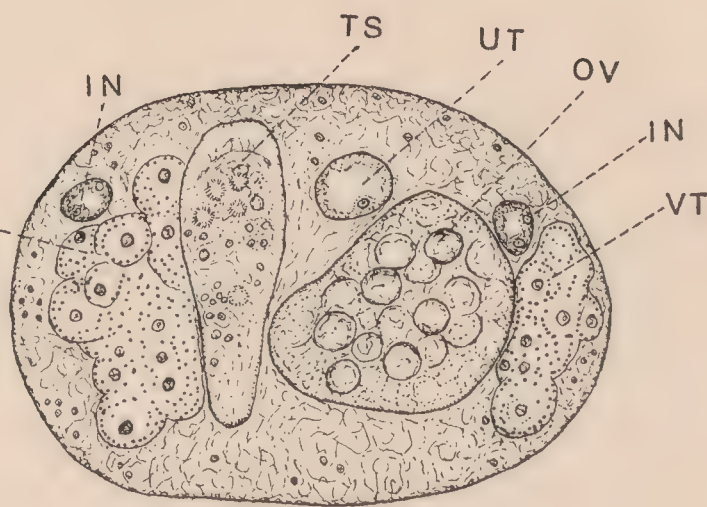


FIG. 60

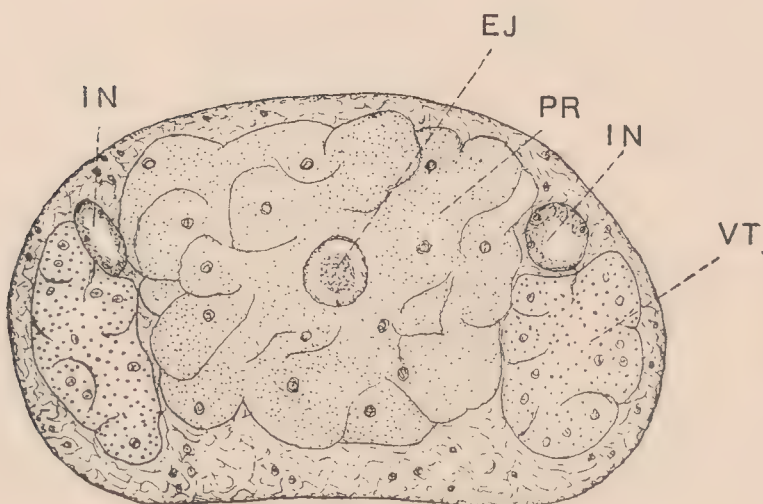


FIG. 57

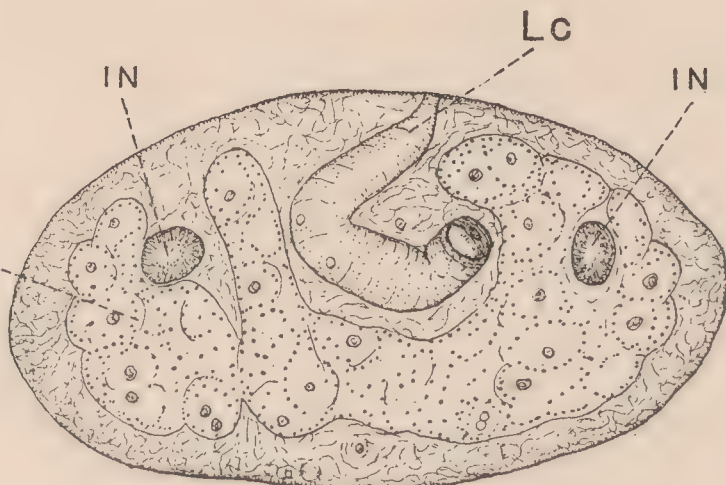


FIG. 61







Article VIII.—A JURASSIC FISH FAUNA FROM WESTERN CUBA, WITH AN ARRANGEMENT OF THE FAMILIES OF HOLOSTEAN GANOID FISHES

BY WILLIAM K. GREGORY

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INTRODUCTION

During the course of Mr. Barnum Brown's explorations in Cuba (1911-1919) he paid special attention to the Jurassic formations of the western province, Pinar del Rio, studying especially the stratigraphic sequence on the southern flanks of the Sierra de los Organos and making large collections of the ammonites and other invertebrates, which have supplied the means of correlating the horizons of the Cuban Jurassic with those of Europe.<sup>1</sup> The horizons range from the Lower Oölitic upward, through the Oxfordian, Corallian, Kimmeridgian and Portlandian.

The fossil ganoid fishes described below were collected by Mr. Brown in the Viñales section. They are found in black limestone accretions, or nodules, sometimes in association with ammonites. At Mina Constancia they are recorded as from the "Lowest Jurassic" but their relationships seem to be rather with Kimmeridgian forms. The fishes were mostly of relatively large size. First, there was a compressed, deep-bodied fish of the genus *Gyrodus*, a large pycnodont, about a third of a meter in length, with round-topped teeth, probably adapted for crushing

<sup>1</sup>Cf. Brown, Barnum, 1919, 'Discovery of the Oxfordian in Western Cuba,' Bull. Geol. Soc. Amer., XXX, p. 152 (abstract).  
Brown, Barnum, and O'Connell, Marjorie, 1922, 'Correlation of the Jurassic Formations of Western Cuba,' Bull. Geol. Soc. Amer., XXXIII, Part 3.



mollusc shells. Next there were several predatory forms of the families Eugnathidæ and Pachycormidæ, one of them being perhaps two meters in length. These all evidently belong in the order Holostei or Protospondyli, together with their modern relatives *Lepidosteus* and *Amia*. A much smaller fish, named below *Leptolepis* (?) species, belongs in the order Isospondyli and represents the early and primitive teleosts.

The fish fauna, so far as known, is typically Jurassic in character. The *Gyrodus* seems to be closely related to several of the many species that occur in the Kimmeridgian of Europe. The *Caturus*, *Sauropsis* (?), *Eugnathides*, and *Leptolepis* (?) are related to European forms that range from the Lower Jurassic upward, some even extending into the Wealden.

Perhaps the most interesting result of the present paper is the additional evidence for the very close relationship of the families Eugnathidæ and Pachycormidæ, as already intimated by Dr. Smith Woodward.<sup>1</sup> The writer's views of the inter-relationships of the various families of the order Holostei are indicated at the close of this paper.

## ORDER HOLOSTEI (PROTOSPONDYLI)

### Pycnodontidæ

#### *Gyrodus macrophthalmus cubensis*, new subspecies

TYPE.—Amer. Mus. Cat. Fos. Fishes, No. 7928 (Field number V 1): vomerine and mandibular dentition.

GEOLOGICAL HORIZON AND LOCALITY OF TYPE.—“Basal levels” of the Jurassic, as exposed one kilometer S. E. of San Vicente, Pinar del Rio, Cuba. Of Kimmeridgian age.<sup>2</sup>

PARATYPE.—Amer. Mus. Cat. Fos. Fishes, No. 7927 (Field number C 1): part of the head with little-worn mandibular teeth and part of the left side of the body showing the scales. From Mina Constancia, six miles N. E. of Viñales.

DESCRIPTION.—Vomerine dentition having the median row equalling or exceeding the two flanking rows in width; crowns of unworn smaller teeth having two concentric mammilate rings and a central papilla; on the larger teeth the papillæ are very numerous and less regular in arrangement, the central papilla and the rings losing their distinctness; all the teeth become smoothly rounded by wear. Body length estimated at about .345 m. Body scales covered with coarse pits, ridges and tubercles, forming a more or less reticular pattern.

The material available indicates that the Cuban species has the central row of vomerine teeth distinctly larger than in *Gyrodus planidens*<sup>3</sup> of Kimmeridgian age. The intermediate row of vomerine teeth is

<sup>1</sup>Woodward, A. S., 1895, 'Catalogue of the Fossil Fishes in the British Museum,' Part III, p. xvi.

<sup>2</sup>Brown, B., and O'Connell, M., 1922, p. 648.

<sup>3</sup>Cf. Woodward, A. S., 1895, 'Cat. Fos. Fishes Brit. Mus.,' Part III, p. 244. (Also contains references to plates in Agassiz and other works examined.)



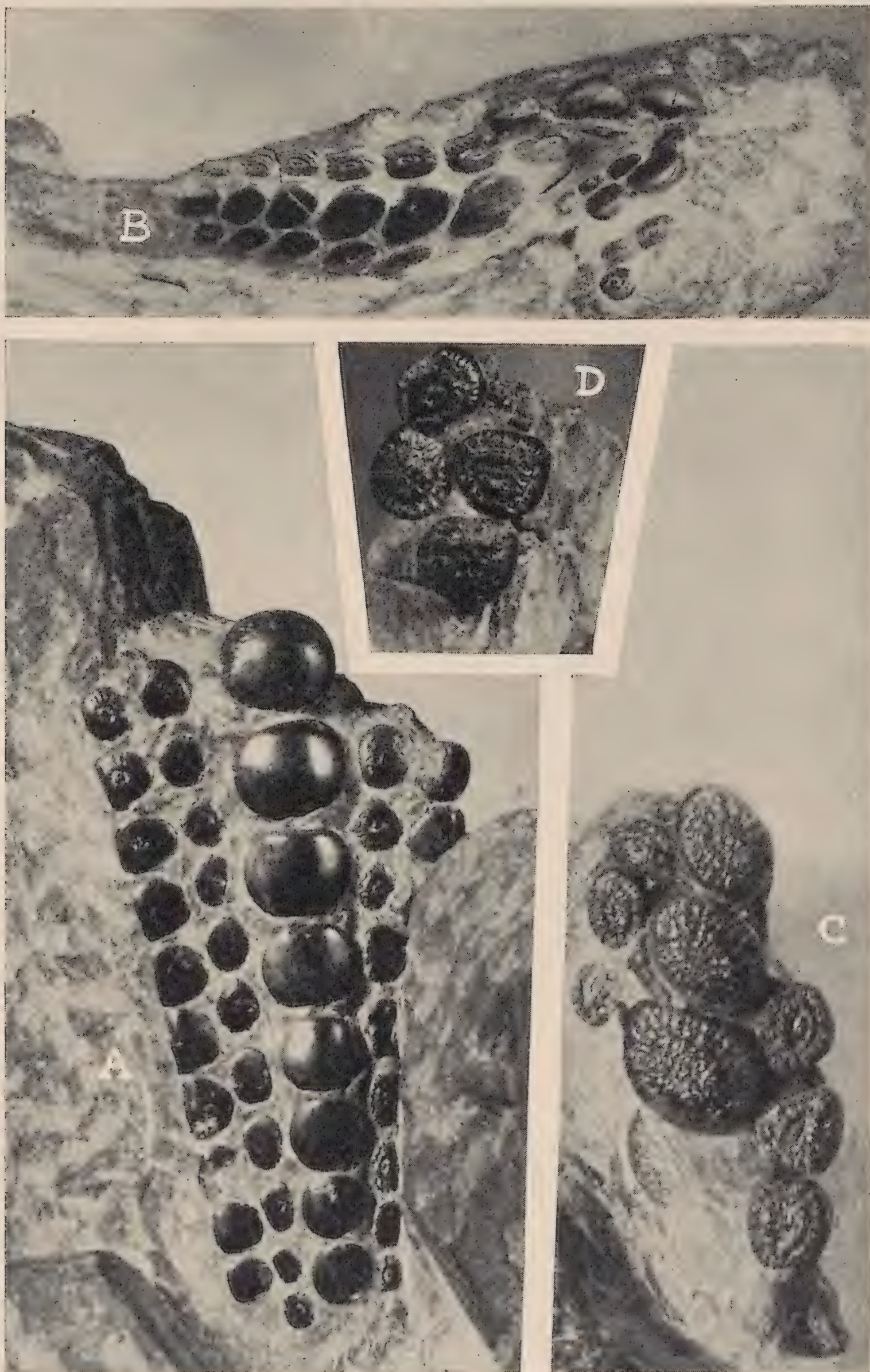


Fig. 1. *Gyrodus macrophthalmus cubensis*.

- A. Vomerine dentition of type (A. M. N. H. No. 7928).  $\times 2$ .  
 B. Mandibular dentition of type, right side, admedial aspect.  $\times 2$ .  
 C. Mandibular teeth of paratype (A. M. N. H. No. 7927) right side. Admedial aspect of upper three rows.  $\times 3$ .  
 D. Vomerine (?) teeth of paratype. The two teeth on the right belong to the marginal row.  $\times 3$ .



smaller than in the Kimmeridgian *G. coccoderma*.<sup>1</sup> The middle papilla in the teeth is less prominent than in the Neocomian *G. minor*.<sup>2</sup> The Cuban species appears also to differ from the Lower Kimmeridgian *G. cuvieri*, in which the median vomerine teeth are not quite equal in width to the two flanking series.<sup>3</sup> It agrees closely with the description of the Lower

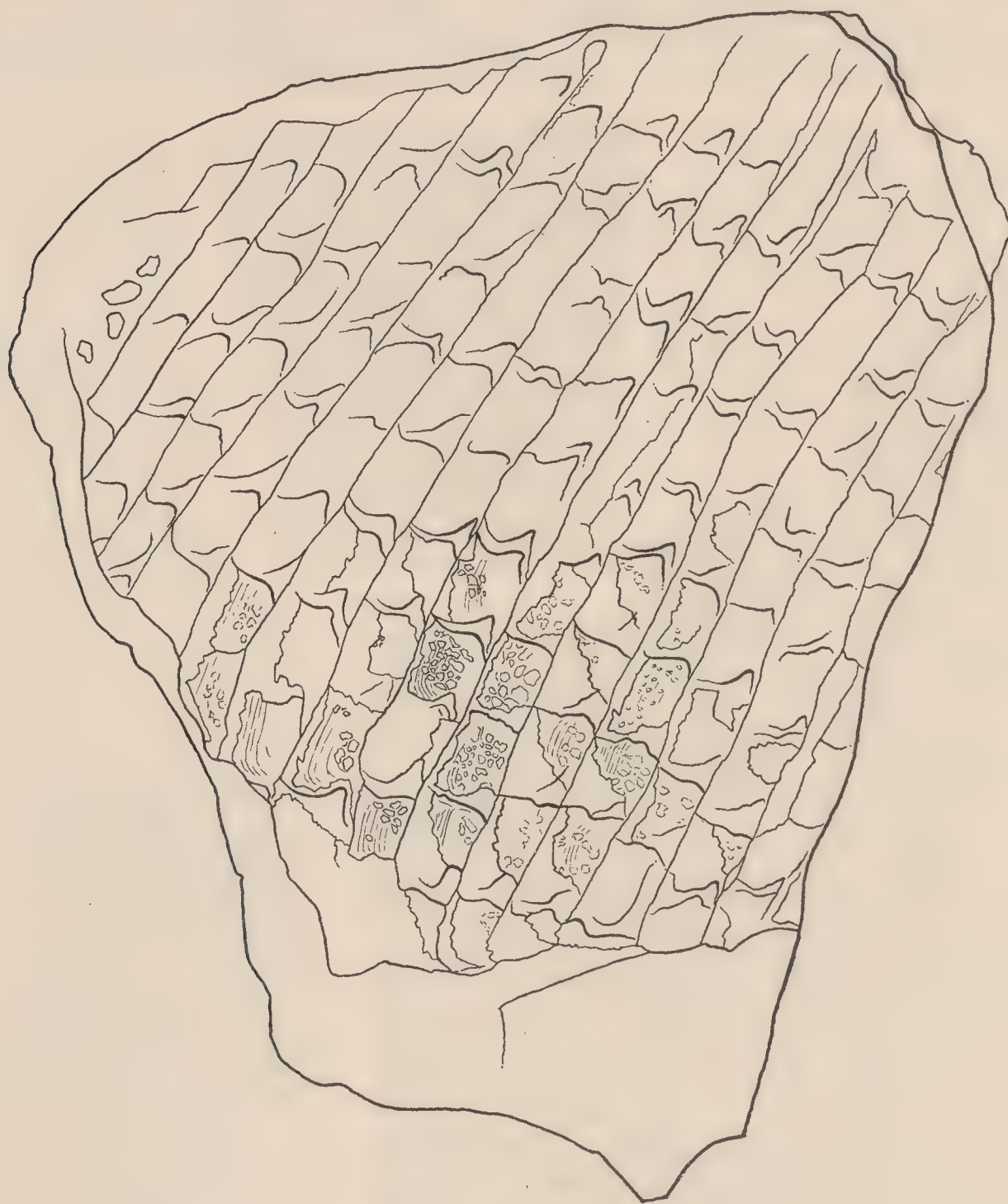


Fig. 2. *Gyrodus macrophthalmus cubensis*.

Part of paratype (A. M. N. H. No. 7927). Fifteen rows of scales covering the lower part of the left surface, extending from just behind the pectoral girdle nearly to the pelvis.  $\times \frac{1}{2}$ .

Kimmeridgian *G. circularis*<sup>4</sup> except that it seems to be much smaller in size (estimated body length .345, as compared with 1 m.) It seems to agree with the largest specimens of *G. macrophthalmus* (also Lower Kimmeridgian) in size and in the general characters of the dentition. It is provisionally assigned as a distinct subspecies of *G. macrophthalmus* on

<sup>1</sup>Cf. Egerton, Sir P., 1869, Quart. Jour. Geol. Soc., XXV, p. 383, fig. 4.

<sup>2</sup>Cf. Woodward, A. S., *op. cit.*, p. 242.

<sup>3</sup>Idem, p. 240.

<sup>4</sup>Idem, p. 238.



account of its wide separation in space from the European form. It may well prove worthy of specific rank when more and better material becomes known.

### Eugnathidæ

#### *Caturus deani*,<sup>1</sup> new species

TYPE.—A. M. N. H. Cat. Fos. Fishes, No. 7930 (C 28): a crushed head, showing especially the outer aspects of the lower jaw, gular plate and branchiostegals; also the premaxilla, maxilla, vomer, orbit, cheek plates, and opercular region.

■ GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic” one mile east of Constanca (near Viñales). Probably of Kimmeridgian age.

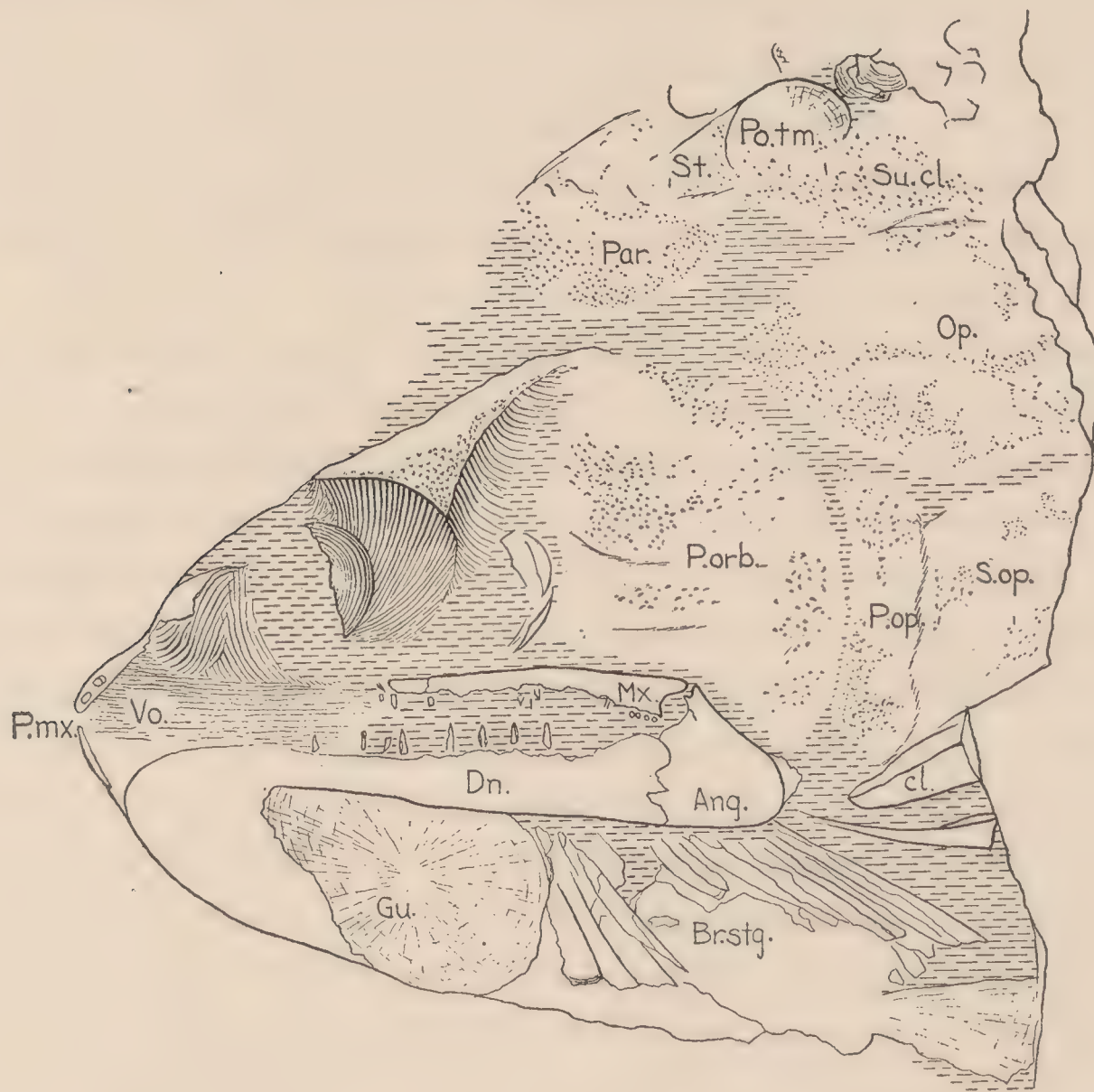


Fig. 3. *Caturus deani*.

Type skull (A. M. N. H. No. 7930).  $\times \frac{1}{2}$ .

REFERRED SPECIMENS.—A. M. N. H. No. 7931 (C 8): a crushed skull, somewhat larger than the type, from the same locality and horizon; A. M. N. H. No. 7933 (C 14) a crushed fish, showing the dorsal aspect of the fore part of the body. Same locality.

DESCRIPTION.—Size large (possibly .7 m. and upward in total length); length of head from tip of snout to posterior border of operculum about .163 m. Gular plate large (.055 in length). Surface of gular plate ornamented with minute pustules. Length of mandible about .095. Opercular region ornamented with fine irregular

<sup>1</sup>Dedicated to my honored preceptor in ichthyology, Professor Bashford Dean.



tubercles and rugæ. Scales (so far as preserved) large, rounded. Maxillary teeth small, slender, numerous, those of the dentary larger, stouter and well spaced, base of teeth not divided. Premaxillary larger than maxillary teeth. Dentary teeth slender, straight, sharply pointed, about 5 mm. in height above the alveolar border, separated from each other by intervals of about  $3\frac{1}{2}$  mm.

As this fish is known only from the head region, such generic and specific characters as would be shown in the general form of body, characters of the vertebræ and tail, proportion of head to body, length, form and position of fins, surface characters of scales, etc., are not presented either in the type or in the certainly referred specimens.

The ordinal relationships of the fish, however, are clear. The fact that it belongs in the order Holostei, or Protospondyli, comprising the existing *Amia*, *Lepidosteus*, and their numerous fossil allies, is shown by the presence in the type and referred specimens of the large gular plate and by the fundamental similarity of all parts of the head to that of *Amia*.

Reference of the Cuban fish to the small-mouthed holostean families Pycnodontidæ, Semionotidæ, Macrosemiidæ, is excluded by the large size of its mouth and by the relatively greater anteroposterior length of the whole head, and especially of the postorbital plates. On the other hand, a reference to the long-snouted families, Lepidosteidæ and Aspidorhynchidæ, is excluded by the normal and unspecialized form of its snout and jaws. Of the three remaining families (Amiidæ, Eugnathidæ, Pachycormidæ), the Amiidæ are at once excluded by their shorter jaws, which are more transversely bowed in front, and usually by their very large cycloid scales. The Cuban fossil is undoubtedly nearer to the Eugnathidæ than to the Amiidæ. Within the Eugnathidæ, *Heterolepidotus*<sup>1</sup> is at once distinguished from the present form by its thick rhombic scales and short operculum; *Allolepidotus*<sup>2</sup> and *Ptycholepis*<sup>3</sup> also have thick scales.

It was at first rather difficult to distinguish the type specimen from the genus *Eugnathus*, with which it agrees in the general characters of the jaws and dentition, but the scales present in the type and referred specimens are relatively large and rounded, instead of small and sharply rhombic, the sclerotic is well ossified and the operculum, at least in the referred specimens, appears to be wider than that of *Eugnathus*. From *Osteorhachis macrocephalus*<sup>4</sup> the Cuban form is distinguished by its more robust jaws, wider operculum, and apparent absence of clustered delicate teeth on the splenial and ectopterygoid (as indicated in referred specimens).

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<sup>1</sup>Woodward, A. S., *op. cit.*, p. 312.

<sup>2</sup>*Op. cit.*, p. 315.

<sup>3</sup>*Op. cit.*, p. 316.

<sup>4</sup>*Op. cit.*, p. 325; also Woodward, A. S., 1895, Geol. Magazine, N.S., Dec. IV, II, p. 204 and Pl. VII, fig. 10.



From most of the numerous species of *Caturus* described by Smith Woodward (*op. cit.*), Agassiz,<sup>1</sup> Thiollière,<sup>2</sup> and others the Cuban fossil differs in its much larger size and in the relative proportions of its jaws and dentition. However, it agrees with *Caturus heterurus*<sup>3</sup> in general characters, especially of the dentition, the maxillary teeth being small, slender and in a close series, the premaxillary teeth larger, the dentary series being the largest of all and comprising slender, well-spaced, straight sharply-pointed teeth, with undivided bases.

The fish as a whole is considerably larger than *C. heterurus*, the estimated total length being about 0.70 as compared with 0.45 in the last-named species. The scales also appear to be relatively larger and more rounded. In the type they are seen only from the inner side and the surface ornamentation is not shown. There are at least seventeen branchiostegal rays preserved (of which the anterior one is 5 mm. wide at the median end) but there were probably not less than twenty-four in all.

In the construction of the mandible and in the characters of the dentition this fish is essentially identical, except in minor details, with the type of *Sauropsis* (?) *woodwardi* described below, but the few scales preserved in the type of *Caturus deani* are relatively large and rounded, while those preserved in the type of *Sauropsis* (?) *woodwardi* are small and rhombic in appearance except on the ventral side, where they are much larger. Again, the close agreements of *Caturus deani* with known specimens of *Caturus*, and of *Sauropsis* (?) *woodwardi* with the less specialized genera of the Pachycormidæ (see below, page 234) suggest that these two Cuban forms really belong to distinct genera. At the same time, the Cuban material reinforces the conclusion already suggested by Woodward<sup>4</sup> that the more primitive Pachycormidæ, such as *Sauropsis*, are only a little more advanced than the more progressive species of *Caturus* of the family Eugnathidæ.

The large scales, very large gular plate, and coarse branchiostegal rays of *Caturus deani*, as well as the rugose ornamentation of the opercular region, thus appear to favor its allocation with the Eugnathidæ rather than with the Pachycormidæ; but the final settlement of this problem requires the examination of specimens that shall reveal the characters of the vertebral column, the form and proportions of the body, and the form and position of the fins.

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<sup>1</sup>Agassiz, Louis, 1833-1845, 'Poissons Fossiles,' I, p. 194, II, pp. 115-119, 164, 165, 293, 294, Tab. 56, 56a. (For further references to Agassiz's plates see Woodward, as cited below.)

<sup>2</sup>Thiollière, Victor, 1873, 'Description des Poissons Fossiles provenant des Gisements Coralliens du Jura dans le Bugey,' pp. 17, 18, Pls. XII, XIII.

<sup>3</sup>Woodward, S. A., *op. cit.*, p. 339.

<sup>4</sup>Idem, p. xvi.



**Pachycormidæ (?)****Sauropsis (?) woodwardi,<sup>1</sup> new species**

TYPE.—A. M. N. H. No. 7934 Cat. Fos. Fishes (C 26): crushed head and pectoral region, showing mostly the inner aspects of the skull, jaws, and opercular region.

GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic, 1 mile E. of Constan-  
cia. Basal 100 ft. and concretions.” (? Kimmeridgian.)

DESCRIPTION.—Head and dentition of eugnathoid type, except that the operculum is wider (width .042) than deep (depth .035). Size large, length of head from tip of rostrum to posterior border of operculum about .145. Surface of opercular region ornamented with fine, irregular tubercles and rugæ. Length of mandible about .095, depth at posterior end .024. Splenial, a large thin plate bearing at most a single row of very fine teeth. Scales on fore part of flanks rhombic, small, becoming larger on ventral surface. Pectoral fins more or less sickle-shaped with about 23 rays which branch only near the distal end. Small pelvic fins located not far behind pectorals. Parieto-occipital protuberance not pronounced. Frontals separate.

**Comparison with the Genera and Species of Eugnathidæ**

This fish differs from *Eugnathus orthostomus*<sup>2</sup> in its non-rectangular operculum, which is wider than deep; its scales, though rhombic, are very small and not strengthened on the inner face with a vertical median rib; the mandible appears to be deeper anteriorly. From *Eugnathus philpotæ*<sup>3</sup> it is distinguished by the much smaller size of the scales and by the elongate operculum, as well as by the ornamentation of the opercular region. It differs from *E. minor*<sup>4</sup> Agassiz in its much greater size, stouter mandible, wider operculum, and smaller scales. From *E. serratus*<sup>5</sup> the species under consideration differs especially in the lesser depth of the abdominal region. It suggests *Eugnathus altus*<sup>6</sup> in the small size and narrowness of the flank scales but differs in the stouter mandible, wider operculum, and far greater size. *E. hastingiæ*<sup>7</sup> is a very small fish with slender jaws; *E. microlepidotus*<sup>8</sup> has large and very robust teeth on the dentary bone, of which there is no evidence in the present species. *E. longiserratus*<sup>9</sup> is a small species with slender jaws, narrow operculum and relatively larger scales. *E. latimanus*<sup>10</sup> is a small fish with a small short head.

<sup>1</sup>Named in honor of Dr. A. Smith Woodward, whose ‘Catalogue of the Fossil Fishes of the British Museum’ is the leading modern work on the evolution and taxonomy of the holostean ganoids.

<sup>2</sup>Woodward, A. S., ‘Cat. Fos. Fishes, Brit. Mus.,’ III, p. 291. (Also gives references to Agassiz and other literature consulted.)

<sup>3</sup>Idem, p. 294.

<sup>4</sup>Idem, p. 296.

<sup>5</sup>Idem, p. 298.

<sup>6</sup>Idem, p. 299.

<sup>7</sup>Idem, p. 299.

<sup>8</sup>Idem, p. 300.

<sup>9</sup>Idem, p. 301.

<sup>10</sup>Woodward, A. S., ‘Cat. Fos. Fishes Brit. Mus.,’ III, p. 302.



From *Heterolepidotus latus*<sup>1</sup> and *H. serrulatus*<sup>2</sup> the present species is excluded by its much smaller scales and longer head; in *H. typicus*<sup>3</sup> the operculum is not so wide. *H. striatus*<sup>4</sup> is a small Upper Triassic species of robust proportions, opercular bones ornamented with coarse rugæ. *H. cephalus*<sup>5</sup> (Upper Triassic) is a very small species in which the operculum is much deeper than broad; the remaining species of *Heterolepidotus*, as described by Smith Woodward,<sup>6</sup> are likewise easily distinguished from the present species.

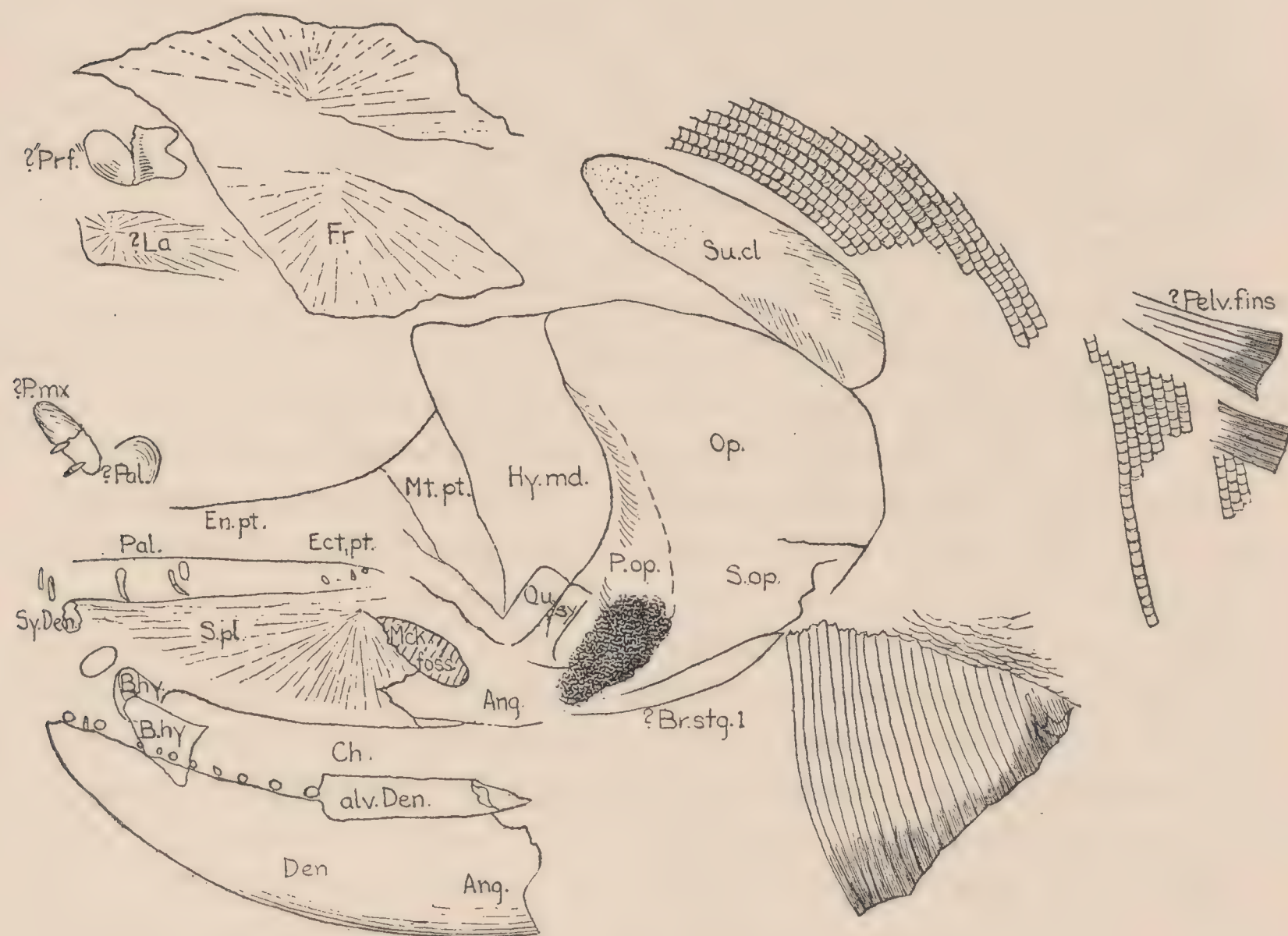


Fig. 4. *Sauropsis* (?) *woodwardi*.

Type, A. M. N. H. No. 7934.  $\times \frac{1}{2}$ .

*Allolepidotus*,<sup>7</sup> an Upper Triassic genus, has a robust form of body and shows no special relationship to *Sauropsis* (?) *woodwardi*.

*Ptycholepis*,<sup>8</sup> from the Upper Trias and Lower Lias, has a highly characteristic surface ornamentation of prominent ridges on the head and in the thick scales.

<sup>1</sup>Idem, p. 304.

<sup>2</sup>Idem, p. 307.

<sup>3</sup>Idem, p. 308.

<sup>4</sup>Idem, p. 311.

<sup>5</sup>Idem, p. 311.

<sup>6</sup>Idem, pp. 312-314.

<sup>7</sup>Idem, p. 315.

<sup>8</sup>Idem, p. 316.



In *Osteorhachis*<sup>1</sup> the operculum is deeper than broad and the scales have a large peg-and-socket articulation, which is not visible in *Sauropsis* (?).

The fish under consideration comes closer to *Caturus*,<sup>2</sup> but differs from it in having small rhombic scales on the fore part of the flank, the operculum is more elongate anteriorly, the mandible stouter; the pectoral fins have a greater number of rays (23:14±). More in detail: *C. furcatus*<sup>3</sup> has large, very numerous teeth and slender jaws; *C. pachyurus*<sup>4</sup> is a small species with relatively larger teeth than in the Cuban fish; in *C. velifer*<sup>5</sup> and *C. drieri*<sup>6</sup> the teeth are very small and numerous, much more so than in *Sauropsis* (?); *C. velifer*<sup>7</sup> is nearly related to *C. drieri* and has slender jaws; in *C. angustus*<sup>8</sup> the head is unknown but the body is much smaller than in *Sauropsis* (?).

*C. heterurus*<sup>9</sup> comes nearer to *Sauropsis* (?) but has a more slender mandible and fewer rays in the pectoral fin; the operculum also is less elongate. *Caturus latipennis*<sup>10</sup> is closely similar to *C. heterurus*; *C. agassizi* may be the young of the latter (Woodward); in *C. insignis*<sup>11</sup> of the Upper Trias the operculum is twice as deep as broad, whereas in *Sauropsis* (?) it is broader than deep. *C. chiotes*<sup>12</sup> has very wide-based, large mandibular teeth, wholly unlike the slender teeth of *Sauropsis* (?); *C. giganteus*<sup>13</sup> has remarkably large and tumid teeth on the maxilla; *C. suchoides*<sup>14</sup> has the maxilla much like that of *C. giganteus* but less deepened behind, dentary attenuated; teeth indented at base (not so in *Sauropsis* (?); in *C. impar*<sup>15</sup> the maxilla is thick and much arched. *C. purbeckensis*<sup>16</sup> is a very small species in which the external bones are without ornament, the mandible very slender; teeth indented.

The type of *Sauropsis* (?) *woodwardi*, as already noted, agrees with that of *Caturus deani* in the fundamental construction of the mandible and dentition, and even of the skull as a whole. The separation of these two forms is rendered further difficult by the characters of specimen No. 7935 (C 22), in which the detailed construction of the mandible and denti-

<sup>1</sup>Idem, pp. 324-326.

<sup>2</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 330.

<sup>3</sup>Idem, p. 332.

<sup>4</sup>Idem, p. 336.

<sup>5</sup>Idem, p. 338.

<sup>6</sup>Idem, p. 337.

<sup>7</sup>Idem, p. 338.

<sup>8</sup>Idem, p. 339.

<sup>9</sup>Idem, p. 339.

<sup>10</sup>Idem, p. 342.

<sup>11</sup>Idem, p. 343.

<sup>12</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 344.

<sup>13</sup>Idem, p. 346.

<sup>14</sup>Idem, p. 346.

<sup>15</sup>Idem, p. 347.

<sup>16</sup>Idem, p. 348.



tion tend to bridge the differences in the type specimens of *C. deani* and *S. (?) woodwardi*. But, on the other hand, the skull top of the annectent specimen distinctly approaches the primitive pachycormid type as figured by Woodward<sup>1</sup> and tends to reinforce the comparison of *Sauropsis (?) woodwardi* with the pachycormid genera *Sauropsis* and *Euthynotus* (see below).

*Callopterus*<sup>2</sup> of the Kimmeridgian and Wealden is a progressive genus pointing toward the Amiidæ; it differs from *Sauropsis (?)* in its deep operculum, shorter jaw and large cycloid scales.

*Eurycormus egertoni*<sup>3</sup> equals or exceeds *Sauropsis (?)* in size, but it has large tuberculate scales, longer jaws with more delicate teeth. *E. grandis*<sup>4</sup> from the Kimmeridge Clay, differs from *Sauropsis (?)* in (a) deeper operculum; (b) pustulate surface of skull; and (c) very numerous fine teeth on maxilla, which is very broad and massive.

*Neorhombolepis*,<sup>5</sup> from the Turonian, has a deep head, slender mandible and wide maxilla; the anterior fin ray of the pectoral fin is greatly enlarged and there are only about thirteen rays on the pectoral fin; all conspicuous differences from *Sauropsis (?) woodwardi*.

The Cretaceous genus *Lophiostomus*<sup>6</sup> is a very small fish with a large depressed head and very large jaws.

#### Comparison with Amiidæ

From all the Amiidæ except *Liodesmus*, *Sauropsis (?) woodwardi* differs in the very small size of the scales which also are not broadly overlapping; the operculum is wider, the mandible less strongly bowed in front and the pelvic fins further forward. *Liodesmus*<sup>7</sup> is a minute amiid with very small scales. Its head, as figured, is not especially like that of *Sauropsis (?) woodwardi*.

#### Comparison with Pachycormidæ

The species under consideration agrees with some of the more primitive Pachycormidæ in having very small scales, pelvics far forward, wide operculum and cheek plates.

From *Hypsocormus*<sup>8</sup> and *Protosphyræna*<sup>9</sup> it is at once excluded by the absence of an elongate rostrum and greatly enlarged vomerine tusks,

<sup>1</sup>*Op. cit.*, Pl. XIV, fig. 1.

<sup>2</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 315; see also Traquair, 1911, 'Les Poissons Wealdiens de Bernissart,' Mém. Mus. Roy. d'Hist. Nat. de Belgique, VI.

<sup>3</sup>Woodward, A. S., *op. cit.*, p. 352; see also Egerton, Sir P., 'Figs. and Descript. Brit. Organic Remains,' Dec. IX, Mem. Geol. Surv., No. 10, Pl. x.

<sup>4</sup>Woodward, A. S., 1890, Geol. Mag., Dec. III, VII, p. 289, Pl. x, figs. 1-8.

<sup>5</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 355.

<sup>6</sup>Idem, p. 358.

<sup>7</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 361.

<sup>8</sup>Idem, p. 390.

<sup>9</sup>Idem, p. 399.



as well as by the form of the mandible and dentition, greater number of rays on the pectoral fin, etc.

It differs from *Pachycormus*<sup>1</sup> especially in having a smaller median eminence on the back of the skull top, in the greater depth and stoutness of the mandible, and in the presence of pelvic fins.

From *Asthenocormus*<sup>2</sup> it is excluded by its far smaller size, by the presence of minute tubercles and rugæ on the opercular region, and by the narrowness of the flank scales.

The type of *Prosauropsis elongatus*<sup>3</sup> from the Upper Lias of Yonne, France, distinctly resembles our fish in its very small scales and in the pectoral fin, which has about thirty rays, unsegmented, and branching only near the border. Nothing is said as to the teeth, but the maxilla is represented in Sauvage's plate as if it were provided with extremely delicate teeth, whereas in our fish there are fair-sized conical teeth preserved on the maxilla and similar but more widely spaced teeth on the dentary; the jaw also in *Prosauropsis* appears to be straighter and less curved along its lower border.

The Cuban fish differs from the Upper Liassic genus *Euthynotus*<sup>4</sup> in its larger size, but shows a fundamental identity in the construction of the jaws and dentition. The principal generic character of *Euthynotus* is the presence of well-developed hypo- and pleuro-centra, surrounding the notochord. As the type of *Sauropsis* (?) *woodwardi* does not show the slightest indications of vertebral rings or half rings, it seems probable that there were no ossifications in the sheath of the notochord.

On the whole, the nearest resemblances of the Cuban fish appear to be with *Sauropsis* Agassiz as defined by Smith Woodward.<sup>5</sup> At least, it appears to agree with it in all the following generic characters: "Trunk elongate-fusiform, laterally compressed [a fair inference from the shape of the head]. Head relatively large, and snout not produced; marginal teeth well spaced. No ossifications in sheath of notochord. . . Pectoral fins large and sickle-shaped, the rays only branching and articulated at the extreme end; pelvic fins small. . . Scales minute, those of the ventral aspect much broader than deep. . ." The remaining seven generic characters of *Sauropsis*, as given by Woodward, are not revealed in the Cuban material.

*Sauropsis* (?) *woodwardi* differs from *S. longimanus* Agassiz in its much larger size, the length of the head with opercular apparatus being

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<sup>1</sup>Idem, p. 380.

<sup>2</sup>Woodward, A. S., 'Cat. Fos. Fishes Brit. Mus.,' III, p. 380.

<sup>3</sup>Idem, p. 376; see also Sauvage, H. E., 1894, Bull. Soc. sci. hist. et nat. Yonne, XLVIII, Pl. I.

<sup>4</sup>Woodward, *op. cit.*, p. 377.

<sup>5</sup>*Op. cit.*, p. 375.



about .140, as compared with about .075 in the latter. It approaches *S. latus* Agassiz<sup>1</sup> in the size of the head but in the latter the pelvic fins arise slightly nearer to the anals than to the pectorals, while in the Cuban fossil, as preserved, they lie near the pectorals.

### Conclusion

More and better preserved material may conceivably prove that the marked difference in the appearance of the scales between the types of *Caturus deani* and *Sauropsis* (?) *woodwardi* is due to different accidents of preservation or to the scales being shown in different aspects.<sup>2</sup> In that event the relationship between the two forms may even amount to identity, especially in view of the annectant characters of a certain specimen mentioned above (A. M. N. H. No. 7935 (C 22)). But meanwhile the differences in the form of the scales in the two types is an objective fact which repeated and critical examination serves only to throw into clearer relief. To describe *Caturus deani* and *Sauropsis* (?) *woodwardi* under a single specific name on the basis of present material would hardly conduce to clearness, since the characters of such a supposed species would be drawn from two lots of material which present either non-homologous parts, or different aspects of homologous parts, or apparently real differences in homologous parts.

In any event, the present material again emphasizes the extremely close relationship of the families Eugnathidæ and Pachycormidæ.

### **Eugnathides browni**,<sup>3</sup> new genus and species

TYPE.—A. M. N. H. No. 7937 (C 21): a crushed head, showing parts of the mandible, maxilla, hyomandibula, operculum, pectoral girdle, and fin, with a patch of the scalation behind the pectoral girdle.

GEOLOGICAL HORIZON AND LOCALITY.—“Lowest Jurassic” (? Kimmeridgian), one mile east of Constancia.

DESCRIPTION.—Size very large. Length of head from operculum to tip of snout estimated at .300—. Head and dentition of primitive pachycormid type; mandible relatively stout, the depth of mandible below posterior end of maxilla being .052. Teeth on dentary close-set, stout, conical, slightly incurved, not divided at base; at least 4 mm. wide at base. Hyomandibular large, directed backward. Pectoral fins with very finely divided rays. Scales very small. Surface of mandible ornamented with minute pustules mostly arranged in rows, which tend to pass into fibrous bony tissue.

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<sup>1</sup>Cf. Woodward, *op. cit.*, p. 376.

<sup>2</sup>Woodward (*op. cit.*, p. 382) has indeed noted that in the genus *Pachycormus*, “the apparent size of the scales differs greatly according to the degree and manner in which they are displaced.” But in the type of *Sauropsis* (?) *woodwardi* the scales of the fore part of the body are not displaced, although seen mostly from the inner side.

<sup>3</sup>Named in honor of Barnum Brown, in recognition of his distinguished services to vertebrate palæontology.



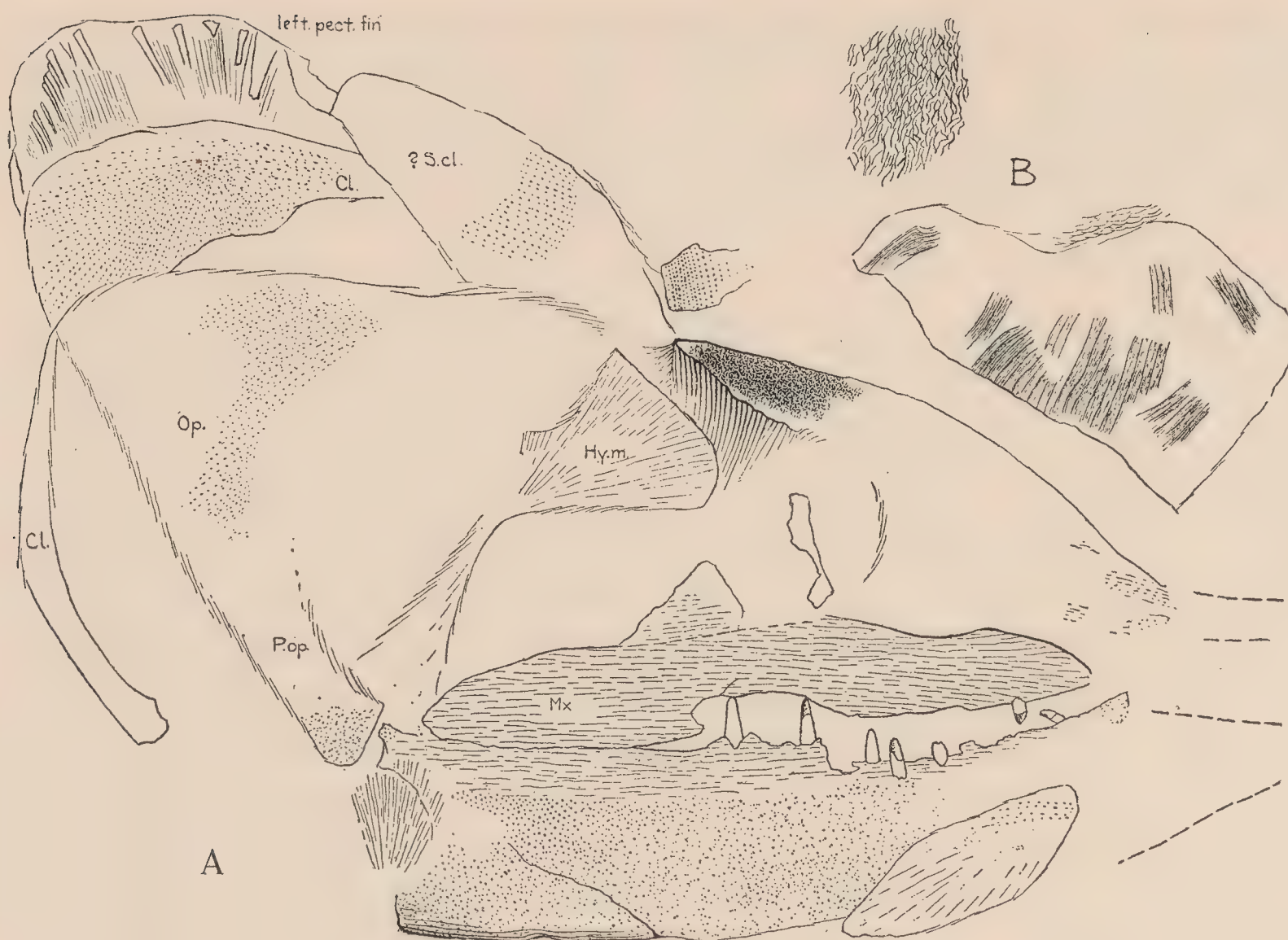


Fig. 5. *Eugnathides browni*.

A. Type skull (A. M. N. H. No. 7937).

B. Portion of right pectoral fin and scalation.  $\times \frac{1}{3}$ .

This large predatory fish is distinguished from *Asthenocormus titan-ius*<sup>1</sup> from the Lithographic Stone of Bavaria, by the presence of minute pustules on the surface (in *Asthenocormus* the surface is described as "fibrous") and by its larger teeth, which in the latter genus are "minute."

It approaches *Sauropsis* (?) *woodwardi* in the very small size of the scales, delicately branched pectoral fin rays and general form of head, but differs apparently in the relatively stouter mandible and in the surface ornamentation, which is more fibrous, with the minute pustules arranged in lines rather than in rugæ.

#### ORDER ISOSPONDYLI

##### Leptolepidæ

##### *Leptolepis* (?) *euspondylus*, new species

TYPE.—A. M. N. H. No. 7939 (C 11): consisting of a crushed head and pectoral region showing several vertebræ, and some slender ribs.

GEOLOGICAL HORIZON AND LOCALITY.—"Mina Constancia, B." (? Kimmeridgian.)

<sup>1</sup>Cf. Woodward, A. S., *op. cit.*, p. 380.



DESCRIPTION.—Notochord persistent, centra consisting of gently constricted cylinders without median lateral ridges. Average length of centra near head 3.8 mm. Ribs slender. Pelvic fins abdominal. Head small.

Relationship with the typical holostean ganoids is definitely excluded by the complete, undivided form of the centra. Relationship with the Oligopleuridæ is excluded by the fact that the vertebræ are not checker-like and the head is small. Relationship with the isospondylous genera *Leptolepis* and *Æthalion* is strongly suggested by the form of the



Fig. 6. *Leptolepis* (?) *euspondylus*.

Type (A. M. N. H. No. 7939), showing outline of skull, ceratohyal, vertebræ, neural arches and ribs.  $\times 1$ .

head, vertebræ, and ribs. The pelvic fins appear to be farther forward than in *Leptolepis*, while reference to *Æthalion* and *Thrissops* is excluded by the lack of median lateral ridges on the vertebræ. Thus the type specimen very possibly represents a new genus, but, as it reveals so few diagnostic characters, it seems better to refer it provisionally to *Leptolepis*.

#### AN ARRANGEMENT OF THE FAMILIES OF HOLOSTEAN GANOID FISHES

The evolution and inter-relationships of the families of holostean or protospondylous fishes were so thoroughly considered by Dr. A. S. Woodward in 1895<sup>1</sup> that the passing years have, for the most part, brought only confirmatory evidence to his conclusions. In the arrange-

<sup>1</sup>Woodward, A. S., 1895, 'Catalogue of the Fossil Fishes of the British Museum (Natural History),' Introduction to III.



ment of these families submitted below I revise and extend my earlier attempt to summarize the main lines of cleavage and adaptive radiation.<sup>1</sup> As the currently recognized families are of unequal phylogenetic value, some being much more nearly related among themselves than to others, an attempt is made to express these relationships by grouping the families into superfamilies. This very convenient taxonomic method was used extensively by the late Theodore Gill, but its advantages seem to have been overlooked by most ichthyologists.

Superclass OSTEICHTHYES

Class Actinopterygii

Order HOLOSTEI

SEMIONOTOIDEA

Semionotidæ

Pycnodontidæ

Lepidosteidæ

AMIOIDEA

Macrosemiidæ

Eugnathidæ

Amiidæ

Pachycormidæ

Order ISOSPONDYLI

PHOLIDOPHOROIDEA

Pholidophoridæ

Leptolepididæ

Oligopleuridæ

*Inc. Sedis*

Aspidorhynchidæ

At the outset we are confronted by the marked difference between English and American systems in the value assigned to the term "order." The system at present adopted by Dr. Smith Woodward sweeps all the hosts of actinopterygian fishes from *Cheirolepis* to *Mola* into a single "order," Actinopterygii, which by Americans is divided into a long series of orders and suborders. As I tried to show in an earlier paper,<sup>2</sup> the practical mnemonic value of bringing the "families" together into larger groups, in accordance with their inferred degree of relationships, seems to counterbalance the objection that, when the families are so grouped into superfamilies and orders, it is often difficult to construct definitions of the larger group which shall be free of exceptions. One way to define one's concept of a group is to list the forms referred to it,

<sup>1</sup>Gregory, W. K., 1907, 'The Orders of Teleostomous Fishes,' Ann. N. Y. Acad. Sci., XVIII, Part 2, No. 3, pp. 437-508.

<sup>2</sup>*Op. cit.*, pp. 437-445.



to state the characters of its more primitive members or of the ancestral forms, to suggest the lines of evolution with reference to conspicuous characters, and to sketch the extreme specializations.

The order Holostei, or Protospondyli, as here limited, starts with *Acentrophorus* of the Permian, which seems to be a forerunner of the better known *Semionotus* of the Trias. As shown by Smith Woodward, these fishes differ from the earlier Chondrostei especially in the abbreviation of the heterocercal into a semi-heterocercal tail, in the loss or absence of "infraclavicles" (clavicles), in the reduction of the pelvic basals to a single piece, and in the equality in number of the dermal rays of the dorsal and anal fins to their endoskeletal supporting elements. The notochord is persistent, the scales rhombic and heavily coated with ganoin; median fins with large fulcra.

This "order" very early divides into two main groups, called here the Semionotoidea and the Amioidea, although one family, the Macrosemiidae, is almost intermediate between the two. A third group, here called the Pholidophoroidea, represents on the whole a distinctly higher grade of organization than either of the others and may best be regarded as a primitive division of the teleostean order Isospondyli, in which even the earliest known forms have an externally homocercal tail, reduced fin-fulcra, and no "splenial" (coronoid) in the mandible.

Among the Semionotidae the oldest form, *Acentrophorus* of the Permian, has a fusiform body with the dorsal fin short and opposed to the space between the pelvic pair and the anal. In *Semionotus* and more advanced genera the body becomes deeper, the dorsal fin lengthens and tends to shift to the posterior slope of the back. The mouth is small, and the suspensorium (hyomandibular) inclined forward. The teeth are at first all styliform but in the more specialized *Lepidotus* those on the roof of the mouth and inner sides of the jaw become flat-topped and tritoral. Finally, the trunk becomes compressed and very deeply fusiform (*Dapedius*) to cycloidal, with protuberant abdomen (*Tetragonolepis*). Range: Permian (*Acentrophorus*) to Upper Jurassic (certain species of *Lepidotus*).

In all the Semionotidae the dermal plates on the side of the head are arranged in concentric series, the first consisting of a row of small circumorbital plates (homologous with the "suborbitals" of Teleosts); behind this is a row of postorbitals ("suborbitals"); the preoperculum and angular form a third curved series; the "supratemporal" operculum, suboperculum, interoperculum, and branchiostegals constitute a fourth, and the post-temporal, supracleithrum, and cleithrum a fifth. While



there is reason to believe that this arrangement is primitive for the whole order, it becomes widely modified in specialized forms.

Remnants of it persist in the Pycnodontidæ, which, as Woodward has shown,<sup>1</sup> are probably "merely extreme members of the modified series of deep-bodied Protospondyli which begins with *Dapedius*," although no real intermediate forms connecting the two families are known. Paralleling in body form the chætodonts, the platysomids and other deep-bodied, small-mouthed fishes, their most conspicuous specialization is the development of a remarkable dental pavement adapted for crushing perhaps small ammonites and other molluscs. The tritoral round-topped teeth are arranged on the vomers in beautifully spaced rows that converge toward the front and are opposed by alternating rows on the inner sides of the lower jaw. In the presumably more primitive species the median row of vomerine teeth do not greatly exceed the flanking rows in width, as they do in the later and more specialized Cretaceous types.

The Eocene to Recent Lepidosteidæ, as suggested by Goodrich,<sup>2</sup> appear to be long-bodied offshoots of the Semionotidæ, which have become secondarily predatory and pike-like. They retain much of the primitive semionotid heritage, especially the forwardly-inclined hyomandibular, the circumorbital plates, the very heavy rhombic ganoid scales, the abbreviate heterocercal tail, and the fin fulcra, as well as other points stressed by Goodrich. They even resemble *Lepidotus* in the loss of a gular plate, although they differ from it in the reduction of the preoperculum and in the concomitant enlargement and substitution for it of the interoperculum. The presence of well-ossified opisthocœlous centra in the Eocene to Recent Lepidosteidæ is no bar to relationship with Triassic semionotids in which the chorda was still present. The Lepidosteidæ differ widely from the amioid family Eugnathidæ in skull characters and still more widely from the Aspidorhynchidæ. One can hardly see why they were ever bracketed with the latter in the highly unnatural "Suborder Aetheospondyli," from which they differ in almost every character except those common to other long-bodied pike-like forms.

The second superfamily, Amioidea, begins with the Upper Triassic to Cretaceous family Macrosemiidæ. These almost divide the differences between the Semionotoidea and the Amioidea, sharing with the former the forwardly-directed suspensorium, although the mouth is

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<sup>1</sup>*Op. cit.*, p. xii.

<sup>2</sup>Goodrich, E. S., 1909, in Lankester's 'Treatise on Zoology,' Part IX, pp. 335, 342-344.



distinctly larger and the body more elongate, as in the Amioidea. In this family the dorsal fin becomes elongate and tends to divide into two, the eye is displaced backward and upward with consequent reduction of the cheek plates, and the ring vertebræ when present often show the alternating pleuro- and hypo-centra that are further developed in the more typical Amioidea. The most central family of the latter is the Eugnathidæ, which are strongly swimming predatory fishes with large mouths, mostly backwardly-inclined suspensorium and sharp teeth on the outer borders of the mouth. With the backward inclination of the hyomandibular the rows of plates behind the orbits are no longer symmetrically arranged; two of the postorbitals become greatly enlarged and partly overspread the preoperculum. The gular plate is large and conspicuous. In the more primitive members the scales are thick and rhombic, in the more advanced they become thin and deeply overlapping. The vertebræ are either unossified or in the form of separate pleuro- and hypo-centra, sometimes fused into rings, rarely in the form of solid discs.

The Pachycormiidæ are advanced to highly specialized derivatives of the Eugnathidæ, forshadowing some of the swifter teleosts of later times and finally giving rise to the long-beaked *Protosphyræna*.

The Amiidæ are long-bodied fishes with the scales usually thin, deeply imbricating and the caudal fin is usually rounded. *Liodesmus* connects them with the Eugnathidæ.<sup>1</sup>

The third group, here called the Pholidophoroidea, is referred to the order Isospondyli.

The most primitive family, the Pholodophoridæ, ranges from the Trias to the Upper Jurassic. The earlier forms resemble the primitive holostean ganoids in their scales, which, however, are overlapping and often have the hinder margin rounded. They differ from the ganoids especially in the loss of the splenial from the mandible. The mandibular suspensorium is nearly vertical or inclined forwards, but the gape of the mouth is fairly wide and often directed somewhat upward. The teeth are small and conical. The premaxillæ are small, the maxillæ large, loosely attached and with two supra-maxillary plates, as in the Leptolepidæ,<sup>2</sup> C. lepidæ, etc. The vertebral centra never advance beyond the annular stage. The tail, although externally homocercal, is not supported by expanded hypural bones (= hæmal arches).

The Jurassic Leptolepidæ are the earliest known true teleosts, with thin cycloid scales, vertebral centra nearly complete, no fin fulcra, inter-

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<sup>1</sup>Woodward, *op. cit.*, p. 360.

<sup>2</sup>Woodward, *op. cit.*, p. 446.



muscular bones present, and head and jaws remarkably like those of primitive Clupeidæ. The homocercal tail sometimes develops hypural bones of primitive teleost type (cf. Woodward, *op. cit.*, Pl. xiv, fig. 7).

The Upper Jurassic and Cretaceous Oligopleuridæ resemble the Amiidæ in their large jaws and large rounded scales, but Woodward (*op. cit.*, p. xx) notes that they differ from the Amiidæ in their completely ossified vertebral centra, which never exhibit alternating pleuro- and hypo-central discs (except on the first vertebra); the mandible appears to lack splenial and coronoid elements and the maxilla bears two supra-maxillary bones " which are arranged like those of Pholidophorus and the Clupeoids" (Woodward, *op. cit.*, p. 492).

The Jurassic and Cretaceous Aspidorhynchidæ were provisionally grouped by Woodward, with the Lepidosteidæ but later authorities (Goodrich, 1909, p. 344, Abel, 1919, p. 212) suggest that they are a long-bodied, long-beaked off-shoot of the Pholidophoridæ. They resemble the latter in their deepened flank scales and homocercal tail and in a few other characters but they retain the ganoidean splenial which is lost in the Pholidophoridæ and related families. Their skull, while more or less ganoid in character, shows no special resemblance to any particular family and the presence and homology of the presymphysial bone of the mandible seems difficult to account for. They are practically *Incertæ Sedis*.



# Article IX.—MUTATION AMONG BIRDS IN THE GENUS *BUARREMON*

BY FRANK M. CHAPMAN

PLATES XIV TO XVII

The question of mutation *vs.* the direct action of environment has recently claimed the attention of ornithologists.<sup>1</sup> Most of those who have expressed themselves in print seem to favor one or the other of these factors, whereas it seems to me that both may be operative. With enormous series of wide-ranging species at his command, the ornithologist is in possession of material to determine the character and extent of the variations in color and in size exhibited by what is obviously the same species. When to this intensive laboratory investigation he adds a knowledge of the environmental conditions under which the species exists, he can often definitely correlate effect and cause.

Thus, he finds large forms occupying colder areas, dark ones humid areas, and pale ones arid areas; and as the conditions which obviously produce these variations in size and color merge one with the other, so do the forms themselves intergrade. That these variations are inherent and not merely the temporary impress of environment on the individual is apparently shown by the fact that they are often as well marked in the nestling as in the adult.

While my experience as a collector and "museum man" has convinced me of the profound influence exerted by observable environmental factors (chiefly climatic) on the species, it has also brought to my attention certain instances in which I believe species have arisen by what is termed mutation, that is, the appearance of characters, great or small,<sup>2</sup> which

<sup>1</sup>Lowe and Mackworth-Praed, *Ibis*, 1921, pp. 344-347; Meinertzhagen, *idem*, pp. 528-537; Bonhote, *idem*, pp. 720-725; Haviland, *idem*, pp. 752-754; *idem*, 1922, pp. 712-715.

<sup>2</sup>The following quotation from an article by Prof. T. H. Morgan, which has appeared since this paper was written, is unusually pertinent in this connection:

"But we also know that minute differences also arise as mutants, and that these are inherited in the same way as are the larger mutant changes. It is also now clear that these smaller mutant variations must be those small heritable variations that Darwin himself appealed to as furnishing the materials for organic evolution. In these respects we have made great advances in knowledge since Darwin wrote; and I doubt if a single geneticist familiar with the evidence at first hand will hesitate to make this substitution. We have learned to distinguish between those individual differences due to the environment (that are not inherited) and those that arise as mutations (that are inherited). Superficially there is no way of telling one from the other, since they overlap and involve the same changes in the same characters. But by pedigree work the essential difference can be made evident, as Johannsen demonstrated in 1909." (*Scientific Monthly*, XVI, No. 3, 1923, pp. 237-246).

"Pedigree work," except with domesticated species, is rarely possible with birds, and such contributions as the ornithologist can make to this subject from a study of birds in nature must be based on the examination of a sufficient number of specimens fully to illustrate the range of a species' variations with an attempt to determine their nature and their causes.

I take advantage of this opportunity to endorse Professor Morgan's "pious wish" (*loc. cit.*, p. 238) for coöperation between geneticists and systematists. After all, both are trying to discover real relationships and if the latter from the nature of their material, the limitation of their methods, and the classifiers' necessity of always making some decision not infrequently reach erroneous conclusions, their handicaps should win for them the assistance rather than the criticism of those who are discovering more certain means for the determination of affinities than are afforded by most museum specimens.



apparently are the expression of an inherent tendency to vary rather than of environment. Such characters are commonly termed "individual variations." They may be manifested by a greater or lesser number of individuals in widely separated parts of the range of the species, and their perpetuation evidently depends upon their frequency and, especially, on an environment which affords sufficient isolation to ensure their preservation.

To determine the causes which create the inherent tendency to vary regardless of environment is a problem which lies within the field of the experimental biologist. We have here only to consider their results.

To this end I present here the results of my researches, in the museum as well as in the field, of the species of the genus *Buarremon*,<sup>1</sup> together with the conclusions which I have ventured to draw from them.

Briefly, we have two groups of birds in the genus *Buarremon*, the members of which are distinguished from one another, primarily, by having a chestnut or a black and gray or black crown and, secondarily, by the presence or absence of a black pectoral band. It is this black collar which is the principal mutant character and which, as I shall attempt to show, appears or disappears purely as an individual variation and without relation to external influences. Its perpetuation or establishment as a specific mark does, however, depend upon environment expressed in what is doubtless the most important external agent in promoting evolution—that is, isolation.

I do not wish to confuse the main issue by presenting too many details. Since, however, mutation as a species-making agent among birds is not generally accepted, it seems desirable to give here all the facts at my command for the consideration of those students who are not prepared to agree with my conclusions.

Furthermore, if my interpretation of these facts is approximately correct, I believe that it will afford a clue to the origin of many types of distinguishing marks among birds the existence of which it is difficult to attribute to even indefinitely prolonged action of external causes.

The two groups of birds with which we are concerned are the following:

GROUP I. (CROWN CHESTNUT)

Section A. (Pectoral Band Present)

*Buarremon brunneinuchus*

Subtropical Zone, southern Mexico to southern Peru.

Section B. (Pectoral Band Absent)

*Buarremon inornatus*

Subtropical Zone, Chimbo Valley, western Ecuador.

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<sup>1</sup>Including also an allied species (*Pipilo torquatus*), which possesses characters commonly accorded generic rank.



## GROUP II. (CROWN BLACK OR BLACK AND GRAY)

## Section A. (Pectoral Band Absent)

*Buarremon assimilis assimilis*.

Temperate Zone, western Venezuela, Colombia and Northern Ecuador.

*Buarremon assimilis nigrifrons*.

Subtropical Zone, southern Ecuador and northern Peru.

*Buarremon assimilis costaricensis*.

Subtropical Zone, southwestern Costa Rica.

*Buarremon atricapillus atricapillus*

Subtropical Zone, northern end of Central Andes, Colombia.

*Buarremon atricapillus tacarcunæ*.

Subtropical Zone, eastern Panama.

*Buarremon virenticeps*.

Southern end of Mexican tableland.

*Buarremon borelli*.

Northern Argentina.

## Section B. (With a Pectoral Band)

*Buarremon basilicus*

Subtropical Zone, Santa Marta Mountains.

*Buarremon phæopleurus*.

Subtropical Zone, Caracas region.

*Buarremon phygas*.

Mountains of northeastern Venezuela.

*Buarremon poliophrys*.

Temperate Zone, eastern Central Peru.

*Buarremon torquatus*

Subtropical Zone, Yungas region, Bolivia.

*Buarremon fimbriatus*

Subtropical Zone, "ravine near Mizque," Bolivia.

## THE FIRST GROUP

*Buarremon brunneinuchus*, a tanagrine finch, is found throughout almost the entire Subtropical Zone from Mexico to Peru, a more extended range, I believe, than that of any other subtropical species. But, in spite of this fact, no race of it is recognized by systematists, excellent evidence that it presents no appreciable geographic variation. In the Chimbo Valley of western Ecuador, however, it is represented by a closely allied but apparently specifically distinct form, *Buarremon inornatus*, and this bird I believe to be a mutant of *brunneinuchus*.

In the color of the upperparts the two birds are exactly alike, olive-green with a rufous-chestnut crown and black forehead and cheeks. Below, *inornatus* has the white areas larger, and it lacks the conspicuous black breast-band which distinguishes *brunneinuchus*.

I have met the last-named species in life in Mexico, Colombia, and Peru, but a field acquaintance with *inornatus* and its haunts seemed



essential to a satisfactory consideration of the relationships of these two birds. This acquaintance it was my privilege to make in August, 1922.

The following facts in relation to the ranges, characters, variations, etc., of these species, are based on a study of 137 specimens contained in the American Museum, sixteen kindly loaned me by Dr. J. Dwight and Dr. Witmer Stone, and five in the British Museum.

***Buarremon brunneinuchus* (Lafresnaye)**

DISTRIBUTION.—*Buarremon brunneinuchus* is found throughout the Subtropical Zone (or usually between the altitudes of 4–5000 and 9000 feet) from the Province of Vera Cruz, Mexico, to southeastern Peru, except in the Santa Marta Mountains of Colombia and the Chimbo-Chanchan drainage system of western Ecuador. In the latter place it is replaced by *Buarremon inornatus*. With many other species or representative forms common to the Subtropical Zone of Costa Rica and Chiriqui and eastern Panama and Colombia, it is lacking in the region between western and eastern Panama where the mountains fall below the altitude which here marks the lower limit of the Subtropical Zone, and it is doubtless also absent from other regions in which the Subtropical Zone is wanting. In short, expressed graphically, if somewhat loosely, the range of *Buarremon brunneinuchus* may be said to be some 5000 miles long and a mile wide.

In view of its wide distribution, its apparent absence from the Santa Marta Mountains of Colombia is significant, and the fact that it is wanting in the Chimbo-Chanchan valleys, where it is replaced by *Buarremon inornatus*, indicates that the latter represents it in that locality. We have specimens from Mindo and from El Chiral, respectively north and south of the range of *inornatus* on the western slope of the Ecuadorian Andes.

HABITS.—*Buarremon brunneinuchus* lives on or near the ground in the dense, luxuriant undergrowth of the Subtropical Zone. It is usually seen along the borders of trails or clearings either because it or the collector selects such situations. Its habits in a general way resemble those of the towhee (*Pipilo erythrophthalmus*) but it is more retiring than that bird, frequents denser growth, and does not range as far above the ground. It is by no means shy and is sufficiently curious to be attracted by the collector's "squeaking," or imitation of the notes of a bird in distress, a fact which has permitted the forming of adequate series of specimens of a species which, if it were wary, would be exceedingly difficult to secure.



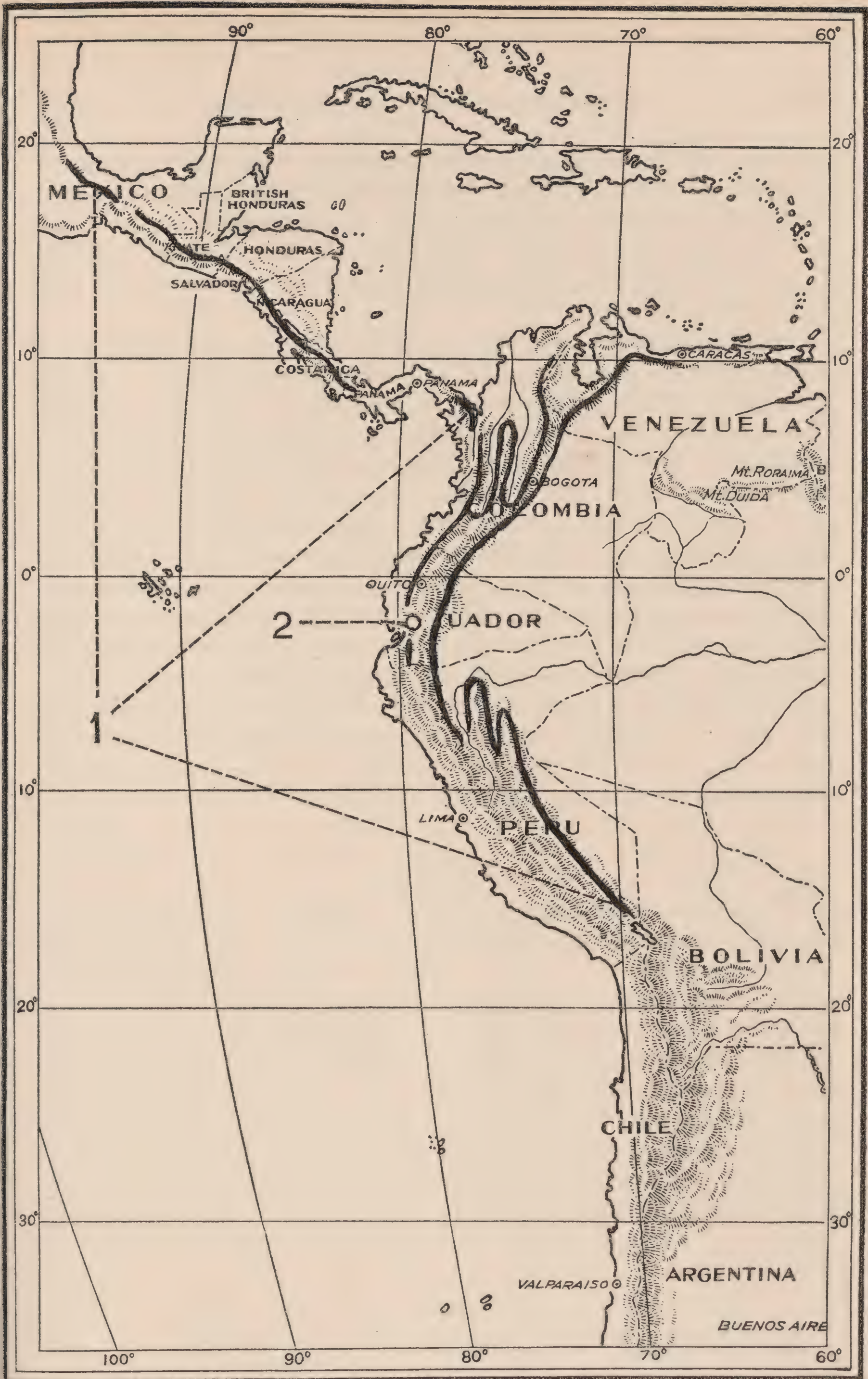


Fig. 1. Distribution of *Buarremon brunneinuchus* and *B. inornatus*.

1. Range of *Buarremon brunneinuchus* in the Subtropical Zone from Mexico to southern Peru.
2. Range of *Buarremon inornatus* in the Chimbo Valley of western Ecuador.



Its call-note, which Stolzmann<sup>1</sup> describes as "tsit-tsit," is not often uttered, and its song, which I have never knowingly heard, is described by the same author as resembling the cry of a rubber doll!

The nest, according to Stolzmann (*loc. cit.*) and Carriker,<sup>2</sup> is placed in low bushes and the eggs, according to the last-named author, are pale bluish white, unmarked.

CHARACTERS OF THE ADULT.—*Buarremon brunneinuchus* is a tanagrine finch about 190 mm. (7½ in.) in length, with the short rounded wing and stout feet of a terrestrial, sedentary bird. In color it is largely olive-green above, with white underparts and a BLACK BAND ACROSS THE BREAST; the forehead and sides of the head are black, with small white marks above the lores and at the base of the culmen; the crown is chestnut-rufous, with a narrow lateral border of ochraceous-orange from above the eye to the nape; the wings and tail are fuscous, edged with olive-green and with bright yellow on the bend of the wing; the sides and flanks are grayish, more or less washed with olive-green; the under tail-coverts are olive-green, usually tinged with brown; and there is often more or less gray on the breast posterior to the black pectoral band.

This description is presented merely to show that both the color and the pattern of *Buarremon brunneinuchus* are sufficiently diversified to offer an opportunity for the display of those variations which it is usual to ascribe to the influence of climatic environment.

### Variations

VARIATIONS WITH AGE.—The juvenal plumage is sooty olive, with a few yellowish streaks on the abdomen, the wings and tail resembling those of the adult. The crown is tinged with dark brown, with a paler lateral margin, suggesting the color and pattern of the adult plumage, but the throat is blackish, darker, therefore, than the remaining underparts; the lower mandible, in three of four specimens, is wholly or largely horn-color or brownish. At the post-juvenal molt the wings and tail are retained, but the rest of the plumage is replaced by that of the adult, from which, at the completion of the molt, the young bird in its "first winter" plumage cannot certainly be distinguished, though in some specimens the lower mandible remains horn-color. It should be noted that the pectoral band is apparently as well developed by this post-juvenal molt as in older birds.

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<sup>1</sup>Orn. du Pérou, II, p. 530.

<sup>2</sup>1910, Ann. Carnegie Mus., VI, p. 899.



SEXUAL VARIATION.—There is no apparent sexual variation in color, but in size males average larger. Eight males and five females from the Western Andes of Colombia measure as follows:

|           | WING    | TAIL    | TARSUS |
|-----------|---------|---------|--------|
| 8 males   | 81–85   | 80–86   | 29–31  |
| 5 females | 78–81.5 | 77.5–81 | 29–30  |

SEASONAL VARIATION.—Forty-one specimens from Colombia (western and Central Andes and western slope of the eastern Andes) represent every month in the year except August. The breeding season, however, evidently extends throughout the greater part of the year and any attempt to determine the yearly range of variation in the color of the plumage of adult specimens must clearly, therefore, be based on the comparison of specimens in similar stages of plumage.

Dissection shows that specimens taken in January, February, March, April, May, June, October, November, and December were breeding. Doubtless this extended nesting season is in part due to local variations in the time of the wet seasons; but the capture of young in juvenal plumage on the western slope of the Central Andes above Palmira in April, and at Salento in September, shows that even under essentially similar climatic control the breeding season covers not less than six months.

Making due allowance for this fact, I am still unable to discover any appreciable seasonal variation in color in this species. In spite of its terrestrial habits, its plumage becomes but little worn, and the nature of its haunts prevents it from being exposed to the sun or to strong light. Freshly plumaged birds show traces of white edgings on the black pectoral band, and their flanks may average greener, but these characters are slight and not constant.

GEOGRAPHIC VARIATION.—The fact that, in spite of its wide range, no geographic races or subspecies of *Buarremon brunneinuchus* are recognized by systematic ornithologists is an eloquent tribute to the stability of the bird's characters. In color, specimens from Jalapa, Mexico, at or near the northern limit of the bird's range, have more gray on the underparts than most specimens from farther south, but they can be matched by others from Chiriqui and Colombia. An excellent series from Nicaragua agrees closely with average South American specimens both in the amount of gray on the underparts and in other respects.

Ridgway,<sup>1</sup> with a series of thirty-eight specimens, including not less than twelve from southern Mexico, states that he is "unable to detect any color differences that can be correlated with geographic areas."

<sup>1</sup>1901, Bull. U. S. Nat. Mus., L, Pt. 1, p. 466.



In size, as in color, this species is notably constant, as the appended table of measurements of thirty males from throughout the range of the species shows. In the mountains of eastern Panama the tail appears to be proportionately shorter than elsewhere, while specimens from southwestern Ecuador average smaller than others in the series.

The bill shows a slight local variation and averages slightly larger and more slender in specimens from near Mérida, Venezuela, and somewhat shorter and proportionately stouter in those from western Ecuador.

MEASUREMENTS OF MALES OF *Buarremon brunneinuchus*

|                                  | WING | TAIL | CULMEN |
|----------------------------------|------|------|--------|
| Jalapa, Mex.                     | 83.5 | 85.0 | 18.2   |
| “ “                              | 84.0 | 84.0 | 18.0   |
| Matagalpa, Nicaragua             | 85.0 | 81.0 | 18.0   |
| “ “                              | 81.5 | 78.0 | 18.0   |
| “ “                              | 86.0 | 84.0 | 19.5   |
| Boquete, Chiriqui                | 83.0 | 80.0 | 18.0   |
| “ “                              | 82.0 | 80.0 | 17.5   |
| “ “                              | 83.0 | 82.0 | 17.5   |
| “ “                              | 83.0 | 84.0 | 18.0   |
| Tacarcuna, E. Panama             | 83.5 | 79.0 | 18.0   |
| “ “                              | 82.0 | 76.0 | 18.5   |
| “ “                              | 83.0 | 78.0 | 19.0   |
| “ “                              | 83.0 | 79.0 | 18.0   |
| San Antonio, W. Andes, Col.      | 85.0 | 83.0 | 17.5   |
| “ “ “                            | 81.5 | 81.0 | 18.5   |
| “ “ “                            | 85.0 | 82.0 | 19.0   |
| “ “ “                            | 83.0 | 81.0 | 18.5   |
| “ “ “                            | 84.0 | 87.0 | 19.0   |
| Mérida, Venezuela                | 81.0 | 85.0 | 19.5   |
| “ “                              | 85.0 | 86.0 | 19.0   |
| Macas, E. Ecuador                | 82.0 | 77.0 | 18.0   |
| “ “                              | 85.0 | 81.0 | 18.5   |
| Zamora, E. Ecuador               | 86.0 | 83.0 | 18.0   |
| Mindo, W. Ecuador                | 83.0 | 82.0 | 17.0   |
| El Chiral, W. Ecuador            | 80.5 | 78.0 | 17.5   |
| “ “                              | 81.0 | 77.0 | 18.0   |
| Near Zaruma, W. Ecuador          | 80.5 | 78.0 | 17.0   |
| “ “ “                            | .... | .... | 17.0   |
| Utcuyacu, Junin, E. Peru         | 81.5 | 78.0 | 18.0   |
| Torontoy, E. Peru                | 83.0 | 85.0 | 18.0   |
| “ “                              | 81.0 | 78.5 | 17.5   |
| “ “                              | 83.0 | 84.0 | 18.0   |
| Santo Domingo, Southeastern Peru | 80.0 | 81.0 | 18.0   |



POSTMORTEM VARIATION IN COLOR.—Under this head I refer only to those changes which occur in specimens of certain birds the exact cause of which is not clearly understood but the extent of which depends upon the age of the skin. Thus, comparison of old "Bogotá" skins collected not less than forty or fifty years ago with others recently collected in the Bogotá region (above Fusugasugá and Buena Vista above Villavicencio) shows that in the older specimens the wings and tail are browner, the back lighter, more yellow-green, the black areas duller. Similar but less pronounced differences exist between specimens collected by de Oca at Jalapa about 1870 and several collected at the same locality by myself in 1897. The latter, however, are paler than specimens collected by Miller and Griscom in Nicaragua in 1917, and doubtless have faded since they were prepared. It is obvious, therefore, that in this species, as in many others, due consideration must be given the age of the specimens when making comparisons. It is, of course, understood that in every instance these specimens have always been stored in light-proof cabinets.

INDIVIDUAL VARIATION.—The variations in the COLOR of *Buarremon brunneinuchus* which cannot apparently be ascribed to age, sex, season, or environment are limited chiefly to the amount of greenish wash on the gray sides and of a brownish tinge in the lower tail-coverts. In PATTERN OF MARKING, including extent of area occupied by certain colors, the variation is greater. Thus, the black band on the forehead ranges from 7 mm. to 12 mm. in width, from the base of the culmen, and rarely its median white line is wanting. In the intensity of the olive-green of the upperparts there is practically no individual variation, but there is a pronounced variation in the amount of gray on the underparts and, particularly, in the width of the black pectoral band.

As has been stated, our Mexican specimens average grayer below than those from farther south, but, aside from this possible geographic variation, there is also much variation among individuals from the same locality in this respect. For example, in a series from Boquete one male is largely gray, another largely white in the region posterior to the black pectoral band. It is, however, in the pectoral band itself that the greatest variation is found. Thus, in a female from Las Lomitas, in the western Andes of Colombia, this band measures approximately 5 mm. in width, whereas in a female from Cerro Munchique, in the same range, it has a width of 11 mm. Again, in males from Chiriqui the band varies from about 5 mm. to 15 mm. in breadth. There is almost as much variation in its lateral extent as in its width. In some specimens it is confluent



with the black of the sides of the head, though usually separated from it by the gray of the sides of the breast or white of the throat.

Variation in this character reaches its extreme in an adult female from Ricuarte, Colombia, in which the pectoral band is not only very narrow but not continuous, the feathers forming its central portion being in part white.

Berlepsch and Taczanowski<sup>1</sup> state that a specimen in the Warsaw Museum, acquired from the elder Verreaux, named by Jules Verreaux "*Buarremon brunneinuchus*," and labeled "Mexico" resembles a specimen of *inornatus* from Cayandeled, Ecuador. It has no trace of a black collar but in size resembles *brunneinuchus*.

Prior to the time in which these authors wrote, *B. inornatus* was known authentically only from the specimens in the British Museum secured by Fraser at Pallatanga in 1858. I am familiar with no record of collections made in the Chimbo Valley between the visit of Fraser and that of Stolzmann and Siemiradski, on whose work Berlepsch and Taczanowski were writing in 1884. This fact, in connection with the statement that the specimen resembles *brunneinuchus* in size, indicates that it is an example of that species in which individual variation in the pectoral band is carried to an extreme, rather than a specimen of *inornatus*; in other words, it is a mutant.

### Summary

1.—*Buarremon brunneinuchus* ranges throughout the Subtropical Zone from Mexico to Peru. It is wanting in the Santa Marta Mountains of Colombia and in the Chimbo Valley of western Ecuador, though found both north and south of that valley in western Ecuador.

2.—It is a terrestrial, sedentary inhabitant of heavily forested regions. The sexes are alike in color, the male being slightly larger. The adult plumage, which is acquired at the post-juvenal molt, is varied in color and in pattern, and presents practically no variations with age or season.

3.—Notwithstanding its exceptionally extended range, the bird exhibits no appreciable variation in color or size which can be correlated with any given area. Fading in color occurs in museum specimens even when they are not exposed to light, its amount depending on the age of the specimen.

4.—Pronounced individual variation is manifest in the extent of the gray or grayish olive areas of the sides and flanks, of the gray on the breast, and in the width and extent of the black pectoral band.

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<sup>1</sup>1884, Proc. Zoöl. Soc., London, p. 292.



***Buarremon inornatus* Sclater and Salvin**

DISTRIBUTION.—Subtropical Zone in the Chimbo-Chanchan river system of western Ecuador in the following localities:

Prov. Chimborazo: Pallatanga, 4950 ft. (3, Brit. Mus.); Cayandeled, 4500 ft. (1, Berlepsch Coll.); Junction Chanchan and Chiguan-cay Rivers, 2500 ft. (3, Acad. Nat. Sci. Phila.); Pagma Forest, 7200 ft. (3, Acad. Nat. Sci. Phila.); Rio Chimbo, 2800 ft. (2, A. M. N. H.); Pallatanga, 4200 ft. 1; 5000 ft., (1, A. M. N. H.). Prov. Bolivar: Porvenir (1, Brit. Mus.). A specimen in the British Museum is recorded in the 'Catalogue of Birds,' as "Jima, Ecuador (Buckley)," but, as Jima is in the Temperate Zone of eastern Ecuador, it is evident that this specimen is among the unfortunately large number of inaccurately labeled birds in the Buckley collection.

The Chimbo separates a spur of the western Andes from the main mountain range. While this spur, known as the Chillanes range does not reach a greater altitude than 8000 ft., it is evident from collections made by Fraser<sup>1</sup> at Chillanes that, in spite of the comparatively low altitude, the fauna of the summit of the range is strongly humid temperate in character, a fact possibly due to the proximity of the snowfields of Chimborazo. This condition creates a measure of isolation in the Valley of the Chimbo and its tributaries which apparently has been sufficiently effective to permit of the development of the characters which distinguish *Buarremon inornatus* from *B. brunneinuchus*.

GENERAL HABITS.—In habits and choice of haunts *Buarremon inornatus* resembles *B. brunneinuchus*. I am not familiar with, and know of no description of its call-notes, song, or nest and eggs.

CHARACTERS.—In the rufous-chestnut crown, bordered with ochraceous-orange, black forehead and sides of the head, olive-green back, etc., *inornatus* exactly resembles *B. brunneinuchus*, but the underparts have more white, the black breast-band is absent, and its size is slightly smaller.

## Measurements

|                                           | WING | TAIL | CULMEN |
|-------------------------------------------|------|------|--------|
| Pallatanga, Ecuador, ♂                    | 74.0 | 73.0 | 18.0   |
| Pagma Forest, Ecuador, ♂                  | 74.0 | 72.0 | 17.5   |
| Rios Chanchan and Chiguan-cay, Ecuador, ♂ | 79.5 | 75.5 | 18.3   |
| Rios Chanchan and Chiguan-cay, Ecuador, ♂ | 79.0 | .... | 18.3   |
| Rios Chimbo and Coco, Ecuador, ♀          | 75.0 | 73.0 | 17.3   |
| Rios Chimbo and Coco, Ecuador, ♀          | 77.0 | 73.0 | 17.3   |
| Rios Chimbo and Coco, Ecuador, ♀          | 74.0 | 71.0 | ....   |
| Pagma Forest, Ecuador, ♀                  | 74.0 | 72.0 | 18.0   |

<sup>1</sup>Sclater, 1860, Proc. Zoöl. Soc., London, p. 1.



VARIATIONS.—Of the sixteen specimens of *Buarremon inornatus* known to me, I have examined all but the male from Cayandede in the Berlepsch Collections. The juvenal plumage, if one may judge from a Pallatanga specimen in the British Museum, resembles that of *B. brunneinuchus*. The sexes are alike in color, but the males average slightly larger in size. The range of the species is too limited to expect it to exhibit appreciable geographic variation, but individually it varies in the extent of encroachment of the greenish gray sides on the white of the underparts and the degree to which a pectoral band is suggested by black-marked feathers on the breast. An adult male in the American Museum taken by George Cherrie, July 31, 1922, has the grayish green sides even more extensive than in average specimens of *brunneinuchus*, while across the breast there are unmistakable traces of a pectoral band. Of six specimens collected by S. N. Rhoads, in the Academy of Nat. Sci. Philadelphia, a male from the junction of Chanchan and Chiguancay rivers has several black-marked feathers in the center of the breast; a second male from the same locality and a male from Pagma Forest show traces of black at the sides of the breast.

#### Summary

1.—*Buarremon inornatus* occupies a limited area in the Subtropical Zone of western Ecuador in which *Buarremon brunneinuchus* is unknown. The latter, however, is found in this zone in western Ecuador both to the north and to the south of the region inhabited by *inornatus*.

2.—The two birds appear to agree in general habits and choice of haunts.

3.—In nestling plumage *Buarremon inornatus* resembles *B. brunneinuchus*.

4.—Adult *Buarremon inornatus* differs from adult *B. brunneinuchus* in the greater expanse of white in the underparts and in lacking a black pectoral band, but individuals occur in which the white area below is of even less extent than in *brunneinuchus* and which show traces of a pectoral band.

Fig. 2. Map illustrating the known distribution of *Buarremon brunneinuchus* and *B. inornatus* in the Subtropical Zone of Ecuador. (See opposite page.)

Black dots (●) localities at which *B. brunneinuchus* has been taken. Note that it occurs in the Western as well as the Eastern Andes, and that it is found both to the north and to the south of the range of *inornatus*.

Circles (○) localities at which *B. inornatus* has been taken. Note that *inornatus* is confined to the Chimbo Valley drainage and that this valley is partly isolated by the main Andean system on the east and the Chillanes range (reaching to the Temperate Zone) on the west.



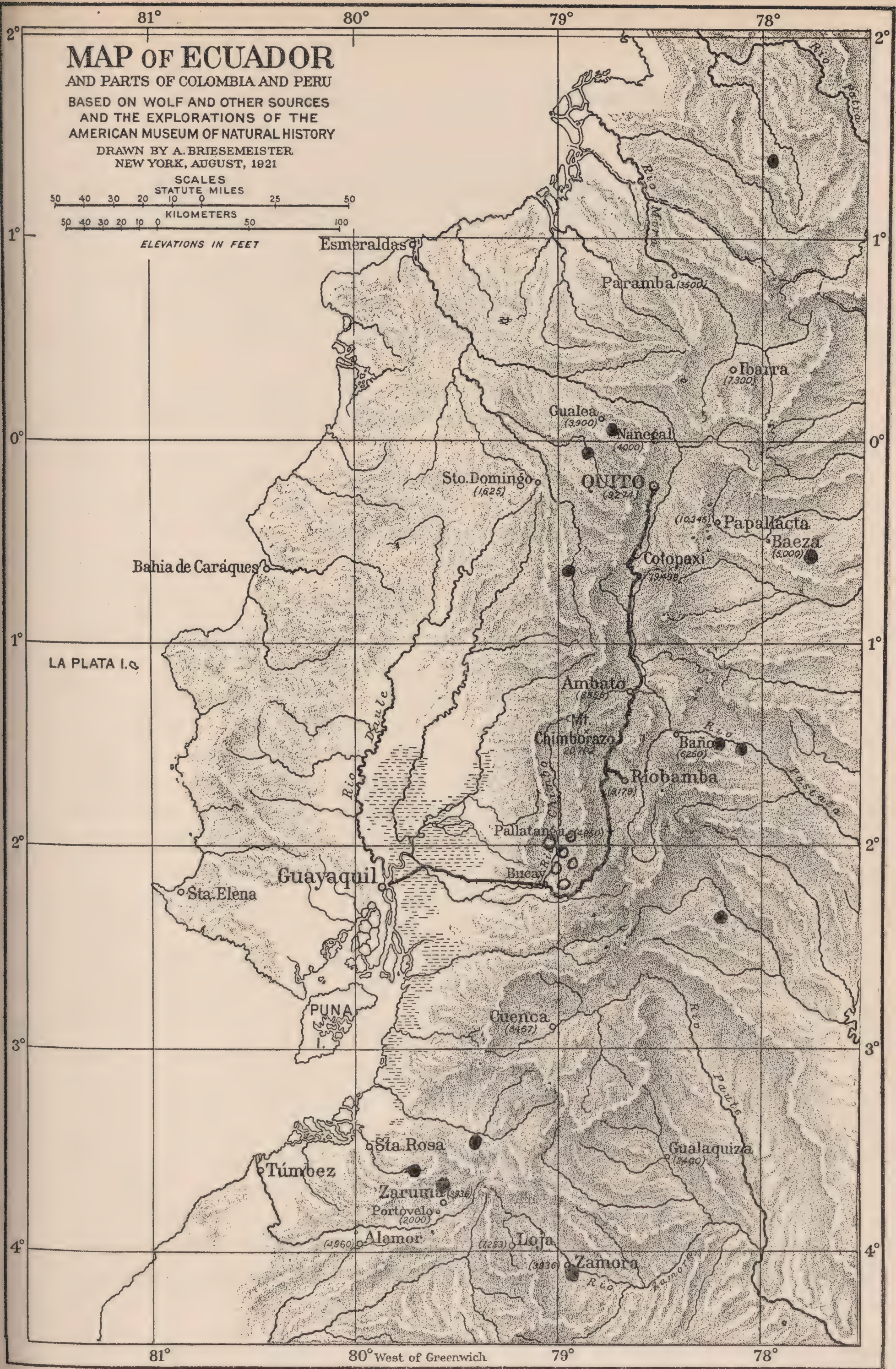


Fig. 2. (For explanation see page 254.)



### Conclusions

The facts above presented appear to warrant the following conclusions.

1.—That *Buarremon inornatus* is a representative of *Buarremon brunneinuchus*.

2.—That the variations in pattern and color occurring in the underparts of *B. brunneinuchus*, throughout the range of that species, are individual and are not due to age, sex, season, climatic, or other observable environmental factors.

3.—That there is an inherent tendency in *B. brunneinuchus* toward the restriction of the grayish colors of the underparts and the disappearance of the black pectoral band.

4.—That isolation, partial or complete, has alone supplied the necessary environmental conditions for the perpetuation of these variations as the specific attributes of *Buarremon inornatus*.

### THE RELATIONSHIPS OF *Buarremon brunneinuchus* TO *Pipilo torquatus*

*Pipilo torquatus* inhabits the Temperate Zone at the southern end of the Mexican tableland. I have taken it at Las Vigas (8000 ft.) in Vera Cruz, immediately above Jalapa (4000 ft.) in the Subtropical Zone, where I found *Buarremon brunneinuchus*. The experience impresses me with the probability that one bird is the zonal representative of the other.

In general appearance *torquatus* closely resembles *brunneinuchus*, but it is a somewhat larger bird with a shorter, stouter bill, heavier feet and less rounded wing, differences which we associate with increase in activity incident to life in a colder region of more open growth.

In color the two birds are strikingly alike, but *torquatus* has more black and less chestnut on the head, the pectoral band is wider, the wings and tail greener, the flanks and crissum browner; in some individuals there are broken blackish malar streaks, the orange-rufous post-ocular stripe is wanting, but there is usually a broad, white, black-streaked superciliary reaching from the base of the bill to the nape.

The replacement of the orange-rufous post-ocular by a white and black superciliary is the most positive character separating the two birds. It is, however, a very variable character and in one of our specimens of the western race of *torquatus* (*alticola*) is represented only by the small white supra-loral spot which is also present in *brunneinuchus*. Another specimen from the same locality (Pisagua, Jalisco) has the superciliary fairly well developed on one side but almost absent on the other, while in our five remaining Jalisco specimens it is present in a variable degree.



We shall find later, in our study of the *Buarremon assimilis* group, that the superciliary is an important, though small, diagnostic mark, distinguishing one form from another but, in this group, also, subject to much variation in individuals from the same locality. While, therefore, we may believe that those differences in size of bill and feet, and in shape of wing which separate *Pipilo torquatus* from *Buarremon brunneinuchus* are the effects of environment acting through habit, and, while those differences of degree which distinguish them in color may also be due to the influence of external causes, the presence of a superciliary, I am convinced, both in this instance and in others to be described beyond, is to be attributed to mutation.

### The Geographical Origin of *Buarremon brunneinuchus*

While this paper is not designed to be a study in distribution, geographical and physical origin are such closely related subjects that one cannot be discussed satisfactorily when the other is excluded. In this connection, for example, it is important for us to consider whether *Buarremon brunneinuchus* is derived from *Pipilo torquatus* or the reverse.

Species occupying the upper life zones in more or less isolated mountain areas are, as a rule, the descendants of forms occupying lower zones. Under the application of this law *Pipilo torquatus* should be derived from *Buarremon brunneinuchus*. The region occupied by *torquatus*, however, cannot be regarded as a more or less isolated mountain zone but rather as a portion of a vast tableland extending northward into the United States, the life of which has been received from the north rather than from the comparatively restricted region lying below it.

Subtropical forms of probable Temperate Zone origin are rare. Probably *Hesperiphona abeillæi* may be so considered and, in my opinion, *Buarremon brunneinuchus* also belongs in this small class.

The fact that in Vera Cruz AND NOWHERE ELSE THROUGHOUT ITS RANGE OF 5000 MILES or more *Buarremon brunneinuchus* has a Temperate Zone representative inevitably leads to the conclusion that the bird has existed longer in Vera Cruz than in any other part of its range.

Whatever may be its physical origin, we may then accept Vera Cruz as the probable region of its geographical origin. From this point it has extended its range southward throughout the Subtropical Zone almost to Bolivia, but IN NO PLACE HAS IT ENTERED THE TEMPERATE ZONE.

On the other hand, *Pipilo torquatus* exhibits characters which indicate that it is an older species than *brunneinuchus*. It includes two forms, and, through *Pipilo nigrescens*, bears relationships to *Pipilo*



*macronyx* which definitely connect it with the great pipeline group. Furthermore, its juvenal plumage emphasizes its affinities with *Pipilo*. There are, indeed, greater differences between *Pipilo torquatus* and *Buarremon brunneinuchus* in juvenal than in adult plumage, a fact for which I am unable to suggest an explanation, though it evidently indicates that the two birds have been separated for a long period.

This brief survey of the relationships of *Pipilo torquatus* and *Buarremon brunneinuchus* leads to the conclusion that the latter is derived from the former, and that the characters separating them are attributable in part to the influence of environment in part to mutation.

### THE SECOND GROUP

The fact that species of the two major groups into which, for convenience, we have divided the members of the genus *Buarremon* are in some instances found associated, together with the differences in color presented by their juvenal plumages, indicates that they represent two distinct branches of the genus.

This second group not only contains a larger number of species than the first, but the evolutionary factors apparently responsible for its differentiations are more numerous and include not only individual variations or mutations, but changes in zonal distribution which present marked differences in environment. There are also present abrupt variations as well as those variations of degree which distinguish what are commonly termed geographical races and which, whatever their origin, do not sharply set one form off from another but connect them so gradually by intergradation through a comparatively wide area that it is impossible to draw a line definitely demarking the range of one form from that of its one or more racial representatives.

As in the First Group, the instance of apparent mutation to which I now wish especially to call attention affects the pectoral band. There are, however, other, though minor, variations to be considered, and all are so closely related and seem to possess so direct a bearing on certain problems of discontinuous distribution in the genus *Buarremon* that it seems essential to review, at least briefly, all the forms of the group.

Fig. 3. Distribution of the gray and black or black-crowned members of the genus *Buarremon*. Note that the areas occupied by species without a breast-band are white, those with a breast-band, black; also discontinuity in the ranges of white-breasted and breast-banded species. (See opposite page.)

1. *Buarremon virenticeps*.

2. *Buarremon assimilis costaricensis*.

3. *Buarremon atricapillus tacarcunæ*.

4. *Buarremon basilicus*.

5. *Buarremon phæopleurus*.

6. *Buarremon phygas*.

7. *Buarremon assimilis assimilis*.

8. *Buarremon assimilis nigrifrons*.

9. *Buarremon poliophrys*.

10. *Buarremon torquatus*.

11. *Buarremon fimbriatus*.

12. *Buarremon borelli*.



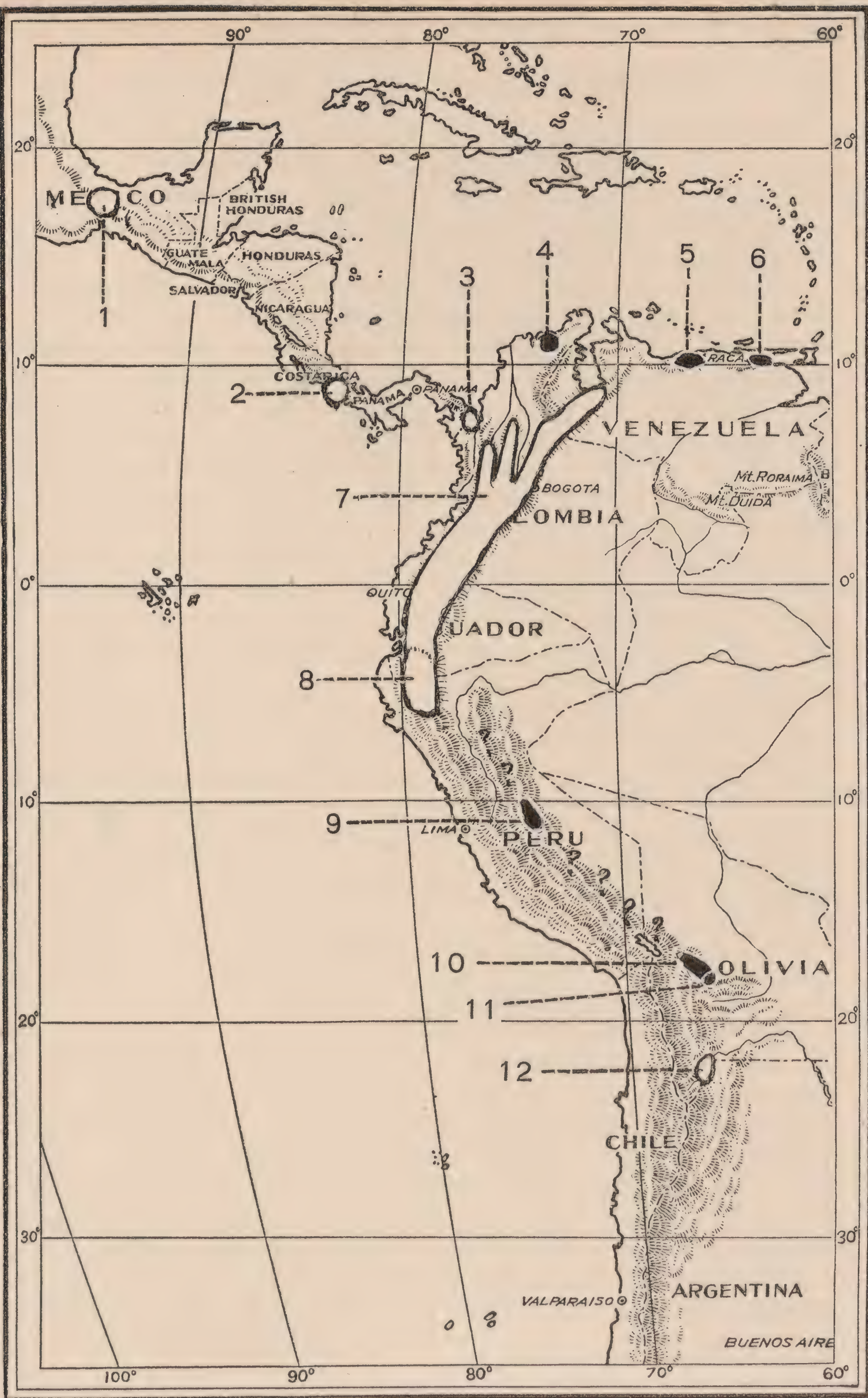


Fig. 3. (For explanation see p. 258.)



## SECOND GROUP; SECTION A. (PECTORAL BAND ABSENT)

The species of the black or black and gray-crowned members of the genus *Buarremon* having white underparts with no pectoral band have a singular distribution (see map).

*Buarremon assimilis*, the most widely distributed form, occupies the Temperate Zone of Colombia and northern Ecuador, the Subtropical Zone of southern Ecuador (where it is represented by the intergrading form *B. a. nigrifrons*), and the Subtropical Zone of southwestern Costa Rica (where it is represented by the intergrading (?) form *B. a. costaricensis*). A distinct white-breasted species (*B. virenticeps*) is restricted to the highlands of southern Mexico, and, after passing in Peru and Bolivia three species with a black breast-band, another white-breasted species (*B. borelli*) is found in northern Argentina.

At the northern end of the Central Andes of Colombia, immediately below the range of *assimilis* in the Temperate Zone, a white-breasted species with a wholly black head (*B. atricapillus*) occupies the Subtropical Zone, and in the same zone of the mountains of eastern Panama this bird is represented by a race, *B. atricapillus tacarcunæ*.

While it is evident that we have here exceedingly interesting problems in distribution and the origin of zonal forms, it seems wise not to pursue this phase of the subject any farther than need be, but to focus our attention on the question of mutation with which we are here especially concerned. Our interest in this connection centers, therefore, on *Buarremon assimilis*, for it is in the heart of the range of this species that the evidence to be considered has been found.

***Buarremon assimilis***

*Buarremon assimilis assimilis* (Boissonneau)

*Buarremon assimilis nigrifrons* Chapman

*Buarremon assimilis costaricensis* Bangs

DISTRIBUTION.—In the Mérida region of western Venezuela,<sup>1</sup> in all three ranges of the Colombian Andes (but not in the Santa Marta group), and southward to northern Ecuador, this species is found in the humid Temperate Zone, that is, between the elevations of, approximately, 9000 and 12,000 feet. In southern Ecuador, however, it occupies the Subtropical Zone. Only one of our thirty-nine specimens from southern Ecuador was taken above an altitude of 7000 feet and the greater number were taken between 2500 and 5000 feet. If all of these specimens were from the Western Andes, we might attribute the lower altitude of their

<sup>1</sup>I have seen no Venezuela specimens.



range to the effects of the Humboldt Current, which markedly lowers the height of zonal boundaries in those portions of western Ecuador to which its influence extends, but since some of our specimens come from as far east as Loja, it is evident that this cool littoral current is not the sole factor which has created the difference in the zonal distribution of this species in Ecuador. But, whatever be the cause, the result is to create a pronounced difference in the climatic environment of the birds of northern and southern Ecuador.

*Buarremon assimilis* belongs in that large group of species which, living above the Tropical Zone in Colombia, are wanting in Panama (except, in some instances, the higher elevations of eastern and western Panama) but appear again in Costa Rica. There, as in southern Ecuador, it is found in the Subtropical Zone, and consequently exists under different environmental conditions from those which prevail in the range of those members of the species which inhabit the Temperate Zone.

HABITS.—In general habits *Buarremon assimilis* resembles *B. brunneinuchus*. Its home is in the dense undergrowth, whether of the humid Temperate or Tropical Zone. It is by no means shy and this fact, in connection with its comparative abundance, makes it an easy bird to secure. Like *brunneinuchus*, it is a silent bird and I have never knowingly heard it either call or sing.

The eggs, according to Stolzmann (Proc. Zoöl. Soc., London, 1880, p. 196), are uniform pale greenish.

CHARACTERS OF THE ADULT.—If one should remove the chestnut cap from *Buarremon inornatus* and give it a black one with more or less gray through the center, at the sides of the neck as well as crown, he would have, essentially, a duplicate of *B. assimilis*. In other words, *assimilis* is a bird with an olive-green back and (externally) wings; a blackish tail; yellow wing-edge; snowy white underparts, with grayish or olive grayish sides; black head and cheeks, with gray markings of variable extent. These variations will be described later.

VARIATIONS WITH AGE.—The juvenal (nestling) plumage, judging from a specimen in the post-juvenal molt, is uniform dull olive-green above, streaked with yellowish below. The black areas in the crown of the adult are a very dark brown, while the adult's gray head-stripes are olive-green. Compared with the juvenal plumage of *B. brunneinuchus*, well-marked differences are noted. The latter is much darker, and less streaked below, and the chestnut cap with its orange-ochraceous border is suggested. These differences serve to emphasize the distinctness of the *brunneinuchus* and *assimilis* groups.



As the post-juvenal molt progresses, black feathers appear and the black crown areas are all well developed before gray replaces the green median and post-ocular stripes. At this stage there is a marked and possibly significant resemblance to the adult of *B. virenticeps* of the southern end of the Mexican tableland.

The plumage acquired by the post-juvenal molt, as with *B. brunneinuchus*, resembles that of the adult.

SEXUAL VARIATION.—The sexes are alike in color but, as in *B. brunneinuchus*, which, it will be observed, this species closely resembles in size and proportions, the male averages larger. The appended measurements were made from specimens taken in the Central and Western Andes of Colombia:

|           | WING    | TAIL  | TARSUS |
|-----------|---------|-------|--------|
| 5 males   | 84–87.5 | 85–92 | 31–32  |
| 5 females | 80–83   | 78–85 | 27–31  |

SEASONAL VARIATION.—Specimens from Ecuador representing eight months of the year show no seasonal variation in color, the effects of neither wear nor fading being noticeable.

VARIATION.—Prior to my study of this group of birds, I should have had no hesitation in labeling as “geographic” certain variations presented by *Buarremon assimilis*. Now I frankly confess I do not know whether to attribute them to the direct action of environment or to the influence of isolation in preserving slight variations produced by internal or germinal, rather than external or environmental, factors.

It is important to remember, however, that both of the slightly differentiated races of *assimilis* of the Temperate Zone inhabit another zone—the Subtropical—and hence are afforded both a different environment and isolation. At the best, the characters separating all three races are slight, and affect chiefly the pattern of coloration of the head. They may be summarized as follows:

#### Characters of the Races of *Buarremon assimilis*

**Buarremon assimilis assimilis.** (Temperate Zone, Colombia and Northern Ecuador.)

Sides of crown and cheeks black; gray median stripe extending FROM THE BILL to the nape, SOMETIMES (about one bird in three) distinctly WHITE at the base of the bill; supra-loral stripe distinctly WHITE, NOT reaching to the bill; post-ocular region gray, broad, widely separating the black aural region from the black crown-stripe.



**Buarremon assimilis nigrifrons.** (Subtropical Zone, Southern Ecuador and Northern Peru.)

Black of sides of crown and cheeks more extensive, gray median stripe narrower usually NOT REACHING IN FRONT OF EYES; white line at base of bill usually present (about 90 per cent of specimens examined); supra-loral stripe distinctly white and reaching almost, if not quite, to the BASE OF THE BILL; post-ocular region gray, narrow, sometimes blackish and then not definitely separating the black aural region from the black crown-stripe.

**Buarremon assimilis costaricensis.** (Subtropical Zone, Southwestern Costa Rica.)

Black of sides of the crown and cheeks much as in *assimilis assimilis*; gray median stripe reaching to the bill; white line at base of bill usually absent; supra-loral stripe GRAY, not reaching base of bill; post-ocular region as in *assimilis assimilis*.

| Variations in Size                        |                  |                  |                  |
|-------------------------------------------|------------------|------------------|------------------|
|                                           | WING             | TAIL             | TARSUS           |
| <i>B. a. assimilis</i> <sup>1</sup>       | 84.0-87.5 (86.0) | 85.0-92.0 (87.0) | 31.0-32.0 (31.2) |
| <i>B. a. nigrifrons</i> , <sup>2</sup>    | 79.0-89.5 (83.0) | 75.0-87.0 (80.0) | 28.0-30.2 (29.3) |
| <i>B. a. costaricensis</i> , <sup>3</sup> | 81.0-86.0 (84.0) | 76.0-81.0 (78.6) | 27.0-28.0 (27.7) |
| CULMEN                                    |                  |                  |                  |
|                                           | LENGTH           | DEPTH            |                  |
| <i>B. a. assimilis</i> <sup>1</sup>       | 17.0             | 7.1- 7.5 ( 7.2)  |                  |
| <i>B. a. nigrifrons</i> , <sup>2</sup>    | 17.3-19.0 (18.3) | 7.7- 8.0 ( 7.4)  |                  |
| <i>B. a. costaricensis</i> , <sup>3</sup> | 18.0-19.0 (18.3) | 8.3- 8.5 ( 8.4)  |                  |

It will be seen that most of the variations in color are not constant. Thus, in all three races specimens from the same place may or may not have a white line on the forehead at the base of the bill, while in two of them the white supra-loral stripe may or may not reach the bill; and in one the gray median line may or may not reach the forehead. In other words, there is sufficient individual variation in specimens from the same locality to bridge their average differences.

Whether variations of this character may be attributed to the action of environment or to an inherent tendency to vary is open to argument. In my belief it is difficult to associate them with the climatic causes we find so potent among song sparrows (*Melospiza*) for example, nor can one

<sup>1</sup>West Colombia.  
<sup>2</sup>Alamor, southwest Ecuador.  
<sup>3</sup>Boruca, southwest Costa Rica.



understand how a climatic environment may affect only certain individuals at a given locality while producing no effect on others.

In size, as in color, it will be seen that, while there are average differences in the length of wing, tail, tarsus, and bill, they are all practically covered by the range of individual variation in only five specimens of each race, but in depth of bill the three specimens of the Costa Rican bird are different from the remaining two forms.

POSTMORTEM VARIATION IN COLOR.—As with *Buarremon brunneinuchus*, skins of *B. assimilis* changed perceptibly with age. "Bogotá" and "Quito" specimens collected probably between 1860 and 1875, when compared with others taken in 1922, have the upperparts much more yellow (approximately the difference between citrine and dark olive-citrine), the tail and wing-quills (except the outer margins) dark sepia (instead of black), the flanks browner.

The differences in color originally attributed to *B. a. costaricensis* were evidently in part due to the use of old "Bogotá" skins in comparison.

INDIVIDUAL VARIATION.—Conscious of the impossibility of drawing a sharp distinguishing line between individual and geographic variations, I pass over here those characters of the crown to which attention has been called and which, whatever be their cause, may be connected with locality, and come at once to the instance which first attracted my attention to the possibility of mutation in this group.

*Buarremon assimilis*, a white-breasted bird, ranges southward to southern Ecuador and the adjoining parts of Peru. But some 300 miles farther south (Maraynioc, Central Peru) it is represented in the Temperate Zone by a bird (*Buarremon poliophrys*) which is exactly like it in color but has a PRONOUNCED BLACK PECTORAL BAND. In other words, the differences between *B. assimilis* and *B. poliophrys* are just the same as those that distinguish *B. inornatus* from *B. brunneinuchus*. It should be added that in its head markings *poliophrys* resembles true *assimilis*, not *assimilis nigrifrons*. That is, the median gray crown-stripe reaches the bill and, in the single specimen I have, the supra-loral stripe does not. In size this bird resembles *nigrifrons* but has a shorter culmen (15.5 mm.).

Most ornithologists have accepted differences of this kind as inexplicable under existing conditions or as possibly the cumulative effects of geographic variations; but, as in the case of *B. brunneinuchus* and *B. inornatus*, specimens recently acquired by our museum lead me to believe that they may be due to mutation. The most interesting of these specimens was acquired in August, 1922, from Mr. Ludovic Söderstrom in Quito. While examining Mr. Söderstrom's collection of birds I found



numbers of specimens of *Buarremon assimilis assimilis* which, like those contained in our own collection, were wholly normal, white-breasted birds, but among them was one with a COMPLETE BLACK BREAST-BAND! The bill agrees with that of *assimilis* but, so far as color is concerned, the bird is essentially *B. poliophrys* of Central Peru.

This specimen (No. 173,089, Amer. Mus. Nat. Hist.) was taken at Nono in the Temperate Zone some fifteen miles northwest of Quito. Normal specimens of *assimilis* were also taken at the same locality. We have one in our collections; while at Verdecocha, about seven miles from Nono, and at approximately the same altitude (9400 ft.), we collected four specimens of true *assimilis*.

It might be suggested that this specimen with the black pectoral band was in truth an individual of the Peruvian *poliophrys* which had wandered far from its own home. But, aside from the fact that in measurements, particularly the size of the bill, the Nono specimen agrees with *assimilis assimilis*, I find that it is not the only specimen in our collections showing the pectoral band which distinguishes *poliophrys* from *assimilis*.

A second specimen was taken by A. A. Allen at Laguneta in the Temperate Zone near the northern end of the Central Andes of Colombia, remote, therefore, from the range of *poliophrys*. In it the pectoral crescent is not complete but is a necklace rather than a band. It is, however, sufficiently developed to be, when considered in connection with the Nono bird, an exceptionally significant variant.

### ***Buarremon atricapillus***

*Buarremon atricapillus atricapillus* Lawrence.

*Buarremon atricapillus tacarcunæ* Chapman.

DISTRIBUTION.—*Buarremon atricapillus atricapillus* is known definitely only from the Subtropical Zone at the northern end of the Central Andes in Colombia, but it may occur also in both the Eastern and Western Andes. Its close relative, *B. atricapillus tacarcunæ*, has been found only in the Subtropical Zone of eastern Panama.

CHARACTERS AND VARIATIONS.—The Colombian form, true *atricapillus*, resembles *B. assimilis* but has the top and sides of the head and nape solid black without median or superciliary stripes, but in one of our four specimens there is, ON ONE SIDE, a trace of a white supra-loral stripe at the base of the bill. The latter member is thicker than in *assimilis* and the culmen is more decurved.

While *assimilis* is presumably a zonal representative of *atricapillus*, the fact that they apparently do not intergrade, though occupying ad-



joining ranges in the same mountain range, indicates their specific distinctness.

*Buarremon atricapillus tacarcunæ* of eastern Panama is more deeply colored above than true *atricapillus*; it has the heavy bill of that form but the head, instead of being black, has gray median and post-ocular stripes as in *B. assimilis nigrifrons*. Three of our four specimens are wholly without a supra-loral stripe. The fourth shows a trace of one, and this specimen, with one other, has a white mark on the forehead at the base of the bill.

If the ranges of *atricapillus* and *tacarcunæ* were reversed, we might well imagine that the latter was a true geographic intermediate between *assimilis* and *atricapillus*, but, as has just been said, the specific distinctness of these two forms is apparently proved by their occupation of adjoining zones without intergrading. We thus have a related but distinct species occupying an area between that of two races of *B. assimilis* (*assimilis assimilis* and *assimilis costaricensis*), a phenomenon I am wholly unable to explain.

#### ***Buarremon virenticeps* Bonaparte**

DISTRIBUTION.—“Southern Mexico in States of Jalisco (San Sebastian), Michoacan (Patzcuaro), Morelos (Huitzilac), Puebla (La Puebla), Mexico (Amecameca, City of Mexico, etc.), and Guanajuato” (Ridgway).

This distant outlier of the *assimilis* group is restricted to the southern end of the Mexican tableland. From between this region and Costa Rica no member of the group has been recorded.

*Buarremon virenticeps* resembles *assimilis* in general coloration. The supra-loral stripes and mark on the forehead at the base of the bill are white, but the post-ocular stripe is greenish yellow, the median stripe is gray anteriorly and yellowish posteriorly, and the breast is more or less grayish. Although obviously distinct, this species appears to be a representative of *assimilis* and the probability of their close relationships is emphasized by the resemblance between *virenticeps* and the juvenal plumage of *assimilis*.

#### ***Buarremon borelli* Salvadori**

DISTRIBUTION.—Known only from San Lorenzo, Province of Jujuy, northern Argentina.

CHARACTERS.—This species, the only member of the genus of which I have seen no specimens, is described as resembling *Buarremon assimilis*, but differing from that species by possessing a conspicuous white super-



ciliary stripe. In the latter character it therefore resembles *B. fimbriatus* of Bolivia, and the fact that in that species the breast-band shows a tendency to disappear suggests that *borelli* may be a mutant, bandless form of *fimbriatus*, just as we believe *inornatus* is of *brunneinuchus*.

#### SUMMARY

1.—The white-breasted, black or black and gray-crowned members of the genus *Buarremon* are distributed discontinuously from southern Mexico to northern Argentina. Species having a pectoral band separate the ranges of those without it.

2.—So far as is known, these birds are sedentary inhabitants of undergrowth and in habits resemble *B. brunneinuchus* and *B. inornatus*. The fact that a representative of this group (*B. assimilis nigrifrons*) is found associated with *B. brunneinuchus*, in connection with the marked differences shown by the juvenal plumages of *brunneinuchus* and *assimilis*, indicates that they belong to distinct branches of the genus.

3.—*Buarremon assimilis*, the most widely distributed species of the group, is composed of three races of which (1) *B. assimilis assimilis* occupies the humid Temperate Zone of western Venezuela, Colombia (except Sta. Marta) and northern Ecuador; (2) *B. assimilis nigrifrons* the Subtropical Zone of southern Ecuador and northern Peru; and (3) *B. assimilis costaricensis* the Subtropical Zone of southwestern Costa Rica, between which region and Colombia the species is unknown.

4.—These forms are differentiated from one another by average differences in the markings of the head and in size, but, with some exceptions, the markings which characterize one race are occasionally exhibited by individuals of one or both of the other races, and, with the exception of the depth of the bill in the Costa Rica race, the average differences in size are bridged by variation among individuals from the same locality.

5.—There is essentially no variation in color with sex or season.

6.—Old museum specimens apparently differ in color from recently collected ones.

7.—A pronounced and significant case of individual variation is shown by a specimen from northern Ecuador which, in possessing a fully developed black pectoral band, exactly resembles in color *Buarremon poliophrys* of Central Peru, while in a specimen from northern Colombia this band is partly developed. In measurements these specimens agree with *assimilis*.

8.—*Buarremon atricapillus atricapillus* inhabits the Subtropical Zone at the northern end of the Central Andes, where its range adjoins



that of *B. assimilis assimilis*. It has a wholly black head and a stout bill, and is evidently specifically distinct from *assimilis*. One specimen out of four examined has a trace of a white supra-loral stripe on one side.

9.—In the Subtropical Zone of eastern Panama *atricapillus* is represented by a race (*tacarcunæ*) with a more deeply colored back and gray head-stripes (much as in *B. assimilis nigrifrons*). The supra-loral stripe is absent except in one of four specimens examined, and this, with one other, has a white line on the forehead.

10.—*Buarremon virenticeps*, of the southern end of the Mexican tableland, is a distinct species with the head-stripes posteriorly yellowish, a character to some extent shown in the juvenal plumage of *assimilis*.

11.—*Buarremon borelli*, of northern Argentina, the most southern member of the genus, resembles *B. assimilis* but has a white superciliary as in *B. fimbriatus*.

#### CONCLUSIONS

Various theories may be presented to explain the distribution of the species of the genus *Buarremon* which are contained in the group we have just considered. I will, however, reserve what I have to say on this subject for a general summing up of the evidence presented by a study of all the species of the genus and confine myself there to a consideration of the variations which we have found to occur in this group of black or black and gray-crowned birds with white breasts having no pectoral band.

1.—While the variations in the color and pattern of head markings in *Buarremon assimilis* are correlated to a large extent with geographic distribution, local variation in them is so great that the markings which characterize one race are often exhibited by one or both of the other races, suggesting that their occurrence is due to an inherent tendency to vary rather than to the direct action of environment.

2.—These variations may, therefore, be considered as slight mutations which, when they occur in a sufficient number of individuals under favorable environmental conditions, become prevalent and characteristic.

3.—The change from the Temperate to the Subtropical Zone in Ecuador and the gap in the range of the species between Costa Rica and Colombia have supplied the isolation from the main range of the species needed for the perpetuation of the differentiating characters exhibited by the southern Ecuador and Costa Rican forms.

4.—The appearance in the heart of the range of *Buarremon assimilis* of an individual of that species possessing a fully developed pectoral



band is an instance of pronounced mutation which demonstrates a potentiality for abrupt variation independent of environment.

5.—The fact that, so far as color is concerned, the acquisition of this band practically changed an individual of *Buarremon assimilis* from northern Ecuador into an individual of *Buarremon poliophrys* of Central Peru, suggests that the latter species is a mutant of the former.

6.—The increase in intensity of color shown by all our specimens of *Buarremon atricapillus tacarcunæ*, of eastern Panama, may well be due to the greater humidity of its range as compared with that of *B. atricapillus atricapillus* of Colombia; but the appearance in the first-named form of gray head-stripes, and in certain individuals of both forms of white supra-loral stripes, is believed to be due to germinal, rather than environmental, influences.

7.—*Buarremon borelli* of northern Argentina is believed to be a representative of *B. fimbriatus* of Bolivia which, as in the case of *B. inornatus*, has by mutation lost its pectoral band.

#### SECOND GROUP; SECTION B. (PECTORAL BAND PRESENT)

Reference to the map will show how widely separated are the ranges of the black and gray-crowned species of *Buarremon* which have a pectoral band.

Thus, *B. basilicus* is confined to the Subtropical Zone of the Santa Marta mountains of northern Colombia, *B. phæopleurus* occupies this zone in the Caracas region, *B. phygas* is found in the mountains of northeastern Venezuela, *B. poliophrys* the humid Temperate Zone of east Central Peru, *B. torquatus*, the Subtropical Zone of the east Andean slopes at Bolivia, and *B. fimbriatus* is known from a single locality in the last-named region.

Further collecting will doubtless considerably extend the known ranges of certain of these species, especially that of *B. poliophrys*, but it is possible that only the ranges of *B. torquatus* and *B. fimbriatus* may adjoin each other.

While these forms bear a general resemblance to one another so close that, if their ranges were continuous, they would probably intergrade, nevertheless, with the possible exception of *fimbriatus* and *phygas*, the characters separating them are sufficiently pronounced to prevent intergradation by individual variation and, taxonomically, therefore, they may rank as "species."

The two exceptions named as possibly intergrading by individual variation more closely resemble one another than do any other birds in



the section; nevertheless, one is found in Bolivia the other in northeastern Venezuela!

From an evolutionary point of view, our specimens of the two Bolivian forms are the most instructive, one of them furnishing an apparent case of the combined effects of mutation and isolation.

Before presenting the evidence on which this assumption rests, we may review briefly the remaining members of this section, beginning at the north.

#### **Buarremon basilicus** Bangs

DISTRIBUTION.—Subtropical Zone, Santa Marta Mountains, Colombia.

CHARACTERS.—Back and wings (externally) browner than in any other member of the genus, between olive-citrine and medal-bronze, rather than olive-green; tail and wings brownish fuscous without olivaceous; median crown-stripe gray, reaching to base of bill; superciliary stripe gray, whiter anteriorly (supra-loral stripe) and reaching to base of bill; sides of the breast gray but flanks and under tail-coverts decidedly brownish; bill long as in *phæopleurus*.

VARIATIONS.—Nine specimens taken from March to June are exceedingly uniform in color, pattern, and size. In one example the central crown-stripe is appreciably whiter at the base of the bill but aside from this the series presents practically no variation.

Doubtless largely because of its practically insular isolation, *Buarremon basilicus* is the most highly differentiated member of this section of the genus.

#### **Buarremon phæopleurus** Sclater

DISTRIBUTION.—Subtropical Zone of the Caracas region, Venezuela.

CHARACTERS.—Back, wings, and TAIL, olive-green yellower than the other forms of the section; central crown-stripe gray; superciliary stripe SNOWY WHITE, both reaching to or nearly to the base of the bill; flanks and lower tail-coverts yellowish or olivaceous old gold; bill large as in *basilicus*.

VARIATIONS.—I have but one specimen of this species and cannot therefore determine its variations. In its white superciliary stripe it resembles *B. phygas* of northeastern Venezuela, as well as *B. fimbriatus* of Bolivia, but it is yellower above than either and lacks the fringed breast-band of *fimbriatus*.



***Buarremon phygas* Berlepsch**

DISTRIBUTION.—Mountains of northeastern Venezuela (Guacharo; Las Palmales).

VARIATIONS.—Back, wings, and tail olive-green, much as in *B. fimbriatus*; head markings also as in that race; the superciliary being white and reaching to the bill; breast-band NOT fringed; bill, small. Of this species I have but one specimen, which, except for its black unfringed breast-band and possibly slightly yellower back, can be closely matched by examples of *B. fimbriatus* of Bolivia.

***Buarremon poliophrys* Berlepsch and Stolzmann**

DISTRIBUTION.—Temperate Zone, east Central (and southern ?) Peru.

CHARACTERS.—Resembling *B. assimilis assimilis* but with a black breast-band and a smaller bill; superciliary gray but with a whitish tendency above the lores, not (?) reaching the bill; median stripe gray reaching the bill and whitish anteriorly; tail blackish.

VARIATIONS.—I have but one specimen of this species the relationships of which to *B. assimilis* have been commented upon under that species.

***Buarremon torquatus* (d'Orbigny and Lafresnaye)**

DISTRIBUTION.—Subtropical Zone, Yungas region, Bolivia.

CHARACTERS.—Back olive-green as in *B. assimilis*; tail BROWNISH BLACK; central crown-stripe gray usually reaching nearly if not quite to the bill and usually whitish anteriorly; superciliary WHITE, NOT reaching to the bill; breast-band, in some specimens, with a slight whitish margin; bill slightly smaller than in *assimilis*.

VARIATIONS.—Eleven specimens taken in May and June at Incachaca (7700 ft.) and Yungas (3600 ft.), department of Cochabamba, are very uniform in general color but present considerable individual variation in pattern. Thus, the median crown-stripe may be continuous or broken; it may or may not reach the bill and the forehead may be black, unmarked, or divided by white or whitish line; the superciliary extends sometimes half-way from the eye to the bill, at others does not quite reach to the anterior margin of the orbit. The black breast-band usually has at least traces of whitish margins, but in some species they are barely evident.

***Buarremon fimbriatus* Chapman**

DISTRIBUTION.—Known only from Tujma (alt. 8200 ft.) "a ravine near Mizque," Dept. of Cochabamba, Bolivia.



CHARACTERS.—Resembling *B. torquatus* but back paler, tail olive-greenish as in *B. phygas* of northeastern Venezuela; superciliary stripe white, REACHING THE BASE OF BILL; breast-band conspicuously margined with white or whitish; flanks and under tail-coverts paler; wings and tail averaging longer, bill shorter.

#### Measurements

| NAME                 | PLACE              | SEX | WING | TAIL | CULMEN |
|----------------------|--------------------|-----|------|------|--------|
| <i>B. fimbriatus</i> | Tujma, Bolivia     | ♂   | 85.0 | 83.0 | 16.0   |
| "                    | "                  | ♂   | 89.0 | 86.0 | 17.0   |
| <i>B. torquatus</i>  | Incachaca, Bolivia | ♂   | 82.0 | 81.0 | 18.0   |
| "                    | "                  | ♂   | 83.0 | 79.5 | 18.0   |
| <i>B. fimbriatus</i> | Tujma, Bolivia     | ♀   | 79.0 | 78.0 | 16.5   |
| "                    | "                  | ♀   | 79.5 | 81.0 | 15.5   |
| <i>B. torquatus</i>  | Incachaca, Bolivia | ♀   | 77.0 | 75.0 | 17.0   |
| "                    | "                  | ♀   | 77.0 | 71.0 | 17.0   |

VARIATIONS.—Aside from differences due to age, eight specimens taken at Tujma in September show little variation in the markings of the head, both central crown-stripe and superciliary reaching the base of the bill in every one of them. There is, however, much variation in the development of the breast-band; in one example it is incomplete, being lacking on the left side and appearing more as a series of disconnected black markings on the center of the breast. It seems probable that, except for the vestiges of the pectoral band, this specimen must closely resemble the white-breasted *B. borelli* of northern Argentina.

Unfortunately, I am not sufficiently familiar with the topographic relations of the ranges of *torquatus* and *fimbriatus* to state whether they are in actual contact or whether the "ravine," in which all our specimens of *fimbriatus* were collected, is cut off from the range of *torquatus*.

It seems evident, however, that *fimbriatus*, like *Buarremon inornatus*, is a highly localized form. While its generally paler coloration may be due to climatic conditions, the pattern presented by the superciliary and fringed breast-band appears to be mutational in character and so clearly to differentiate this form from *torquatus* that not one specimen in our series of nineteen suggests intergradation between the two.

#### SUMMARY

1.—The ranges of species of the genus *Buarremon* having a black and gray head and a breast-band are, with one possible exception, discontinuous. Between the ranges of the northern and southern species, forms without a breast-band occur.



2.—Although representative and closely related, none of the forms of this section is known to intergrade and, taxonomically, they therefore may rank as species.

3.—The species most nearly resembling each other are *phygas* of northeastern Venezuela and *fimbriatus* of Bolivia.

4.—*Buarremon basilicus* of the Santa Marta Mountains is the most strongly differentiated form of the black and gray-crowned group; it shows but little individual variation.

5.—*Buarremon phæopleurus* of the Caracas region and *B. phygas* of northeastern Venezuela are nearly related but are geographically isolated from each other and do not intergrade.

6.—*Buarremon poliophrys* of eastern Central Peru differs from *B. assimilis assimilis* only in possessing a breast-band and smaller bill and may be a mutant form of that species.

7.—*Buarremon torquatus*, of the Yungas region of Bolivia, has the blackish tail of *assimilis*, but the superciliary—which does not reach the bill—is white and the breast-band is more or less fringed.

8.—*B. fimbriatus*, though geographically very near, seems specifically distinct from *torquatus*, of which it may be a localized mutant. It has an olive-green tail, a fringed breast-band and the white superciliary reaches the eye.

#### CONCLUSIONS

1.—That, although differing from the members of Section A of Group II in possessing a black breast-band, the members of this section are nevertheless representatives of the members of that section.

2.—That the differences between the members of Section A and Section B are due to mutation.

3.—That the differences between the members of Section B are in part due to the direct action of environment, in part to mutation, both being made effective by isolation.

#### GENERAL REMARKS

The summaries and conclusions already presented leave little to add to what I have previously said, so far as the genus *Buarremon* is concerned. It remains, therefore, only to comment briefly on what I believe to be the bearings of the facts presented on the study of the evolution and distribution of birds. I intentionally avoid here any discussion of the possible action of natural selection in establishing the characters which distinguish the forms of the genus *Buarremon*. Believing, however, that the presence or absence of a pectoral band, vertical streak, or super-



ciliary line does not materially affect a species' chances of success or failure, I also believe that natural selection has played no part in their development.<sup>1</sup>

There are among birds certain types of markings affecting definite areas which are of such common occurrence that they have received distinctive names in descriptive ornithology. Thus, we have such familiar terms as superciliary stripe, orbital ring, nuchal band, wing-bars, malar streak, pectoral band, etc. These marks occur in birds of widely separated groups, and their presence does not, therefore, necessarily indicate degree of relationship in the birds possessing them. The pectoral band or crescent, for example, is found in several plover, in woodpeckers (*Colaptes*), shore-larks, the meadowlark, finches (*Rhynchophanes*), swallows (*Riparia*), warblers (*Compsothlypis*, *Wilsonia*), and thrushes (*Ixoreus*), to mention only a few instances among North American birds.<sup>2</sup>

Hundreds of other cases might be cited, were it necessary, to illustrate the recurrence of these familiar types of markings among distantly related birds. It is evident, therefore, that, just as we find barred, streaked, or vermiculated feathers, throughout the Class Aves, so, independent of relationships, there also exist certain kinds of markings which affect not single feathers but definite areas. Doubtless there is as deep-seated a physiological reason for the existence of a superciliary stripe in birds as there is for an eye-brow in man, but how it or other recurrent markings came into existence we have yet to learn. This is a problem to which Dr. Witmer Stone<sup>3</sup> has called attention, and toward the solution of which Dr. Glover M. Allen<sup>4</sup> has made a notable contribution.

We are here, however, less concerned with their cause than with their existence in many and very different kinds of birds, of widely different habits, living under widely varying conditions. It is also a fact that these markings are subject to much individual variation and that they may appear sporadically. The white eye-ring and post-ocular stripe of the common murre (*Uria troile* "*ringvia*"), the more or less complete pectoral band found in certain individuals of the piping plover (*Ægialitis meloda* "*circumcincta*"), and the white post-ocular stripes in some in-

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<sup>1</sup>In other words, I consider these markings as representing the "trivial, superficial characters that have, so far as known, no survival value" to which Morgan refers in the paper already cited (Science Monthly, XVI, No. 3, 1923, p. 241).

<sup>2</sup>Compare also Morgan's remarks on the occurrence of the same mutation in different species (*loc. cit.*, p. 247).

<sup>3</sup>1912, 'The Phylogenetic Value of Color Characters in Birds,' Journ. Acad. Nat. Sci., Phila., Ser. 2, XV, pp. 311-319.

<sup>4</sup>1914, 'Pattern Development in Mammals and Birds,' Amer. Nat., XLVIII, pp. 385-412; 467-484; 550-556. Also 1920, 'Pattern Development in Teal,' Auk, XXXVII, pp. 558-564.



dividuals of the blue-winged teal (*Querquedula discors* "albinucha"<sup>1</sup>) are such pronounced instances of this kind of variability that the variants have been described as new forms.

The blackish band which appears on the breast of some individuals of the northern parula warbler,<sup>2</sup> the black crown, sometimes dotted with white, which occasionally is worn by female yellow-bellied sapsuckers,<sup>3</sup> are further instances among many which might be cited of individual variations, or mutations, which, either because they are too infrequent or because the isolation needed for their perpetuation is lacking, have not become fixed.

The species of the genus *Buarremon* supply us with what I believe to be an essentially similar kind of variation, but the mountainous region they inhabit, either through secluded subtropic valley or isolated temperate area, has afforded the environment essential to its perpetuation. Whatever may be the origin of the pectoral crescent in this genus, environment is not now believed to play any part in its presence or absence. It may have developed cumulatively through the preservation of small variations, due to an inherent, unexplained tendency to vary. It may have come into existence full-fledged, just as suddenly as, in the case of *Buarremon inornatus*, it has disappeared. However this may be, a study of our material convinces me of its mutational character, and, if this view should prove to be correct, it will afford a clue to the origin of many differences in pattern of coloration which serve to distinguish one species of bird from another.

Aside from expressing the combined effects of variability and isolation, the presence or absence of a pectoral band may have no faunal significance. Hence, the occurrence of breast-banded Buarremons in Venezuela and Bolivia is to be attributed to parallelism rather than to any more or less direct faunal relation between these two regions.

By parallelism also I would explain the presence of a white-breasted species in northern Argentina and again in Ecuador and Colombia. Thus parallelism may account for many cases of apparent discontinuous distribution, and the faunalist must beware lest he interpret resemblances as relationships and give to them a significance they do not possess.

Less striking than the appearance or disappearance of the pectoral band in *Buarremon*, but no less important, are the variations in the crown, superciliary, and supra-loral stripes, and in the fringe on the

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<sup>1</sup>Cf. Kennard, 1919, Auk, XXXVI, p. 455; Arthur, 1920, Auk, XXXVII, p. 127; Allen, 1920, Auk, XXXVII, p. 558.

<sup>2</sup>Cf. Miller, 1909, Auk, XXVI, p. 309.

<sup>3</sup>Out of 104 females in the collections of the American Museum and Dr. J. Dwight, 9 have black (instead of red) crowns and of these 6 have the crown more or less spotted with white.



breast-crescent. The resemblance in crown-markings between *Buarremon atricapillus tacarcunæ* of eastern Panama and *B. assimilis nigrifrons* of southern Ecuador, and the possession of a similarly extended superciliary in *B. fimbriatus* of Bolivia and *B. phygas* of northeastern Venezuela, may be accepted as instances of parallelism founded on a common ancestry and expressed through an inherent tendency to vary along certain lines; while in the fringed breast-band of *fimbriatus* we find the consummation of a character hinted at in *torquatus*.

The uniformly deeper coloration of *tacarcunæ* of Panama, and *basilicus* of Santa Marta, or the paler hues of *fimbriatus*, from a ravine on the east Bolivian highlands, may be attributed to the direct action of the existing climatic environment, but it is difficult to see any direct relation between environment and the presence or absence of a pectoral band or superciliary stripe. In general tone of color all the forms of the genus present only slight, indeed almost negligible, variation, but, as has been shown, there is wide variation in the pectoral band and head markings among birds from the same locality. These variations, therefore, are individual, not geographic or racial, and consequently may be attributed to internal or germinal, rather than to external or environmental, influences.

Nor are variations manifested only in what may be termed the stereotyped or unit characters of pectoral band, or superciliary streak, etc. They may affect the markings of the individual feather and thus materially alter the pattern of coloration of certain parts of the birds' plumage while leaving the balance wholly unchanged.

For example, a goatsucker (*Systellura ruficervix ruficervix*) of the Temperate Zone from northern Peru to western Venezuela has numerous rounded ochraceous spots on the upperparts, while a representative of it which we have recently discovered in the Temperate Zone of eastern Peru has essentially similar marks but with black centers. This variation might be considered as due to some unknown environmental factor did we not find in our large series of true *ruficervix* a specimen from near Bogotá, Colombia, marked much like the Peruvian bird. Hence it seems most probable that this is an individual or mutational rather than a geographical variation.

To replace the latter term with the former may not advance our knowledge of the fundamental causes of evolution in birds. If, however, while confessing our ignorance of the underlying factors, we admit that variations great and small may arise independently of any observable, external cause, and that chiefly through isolation, partial or complete,



these variations (or mutations) may prevail as specific or subspecific characters, I am convinced that in some cases, at least, we shall have a demonstrable explanation of the origin of the species distinguished by such characters.

#### LIST OF SPECIMENS EXAMINED

##### **Buarremon brunneinuchus.**

MEXICO: Jalapa, 4400 ft., 8.

NICARAGUA: San Rafael del Norte, 4200 ft., 8; Mombacho, 3600 ft., 3; Muy Muy, 1; Rio Tuma, 1; Rio Coco, 1; Ocotal, 1; Peña Blanca, 1; Chontales, 1; Matagalpa, 2200 ft., 6.

COSTA RICA: Navarito, 4000 ft., 2; Aquinares, 4000 ft., 4; Bonilla, 2000 ft., 3; Agua Caliente, 4500 ft., 1.

PANAMA: Boquete, Chiriqui, 14; Tacarcuna, 4600 ft., 16.

COLOMBIA: Western Andes, San Antonio, 7; Las Lomitas, 1; La Florida, 2; Gallera, 2; Cerro Munchique, 2; Ricuarte, 2; Central Andes, above Palmyra, 6800 ft., 4; Salento, 7000 ft., 4; El Roble, 7200 ft., 1; Sta. Elena, 9000 ft., 2; El Eden, 8300 ft., 1; La Candela, 6500 ft., 3; Eastern Andes, Andalucia, 3000 ft., 4; Aguadita, above Fusugasugá, 6500 ft., 3; Buena Vista above Villavicencio, 2; Bogotá, 2.

VENEZUELA: Culata, 9000 ft., near Mérida, 3; Escorial, near Mérida, 8000 ft., 2.

ECUADOR, WESTERN: Mindo, 4400 ft., 1; El Chiral, 5350 ft., 4; above Zaruma, 6000 ft., 2; Salvias, 6600 ft., 1. EASTERN: above Zamora, 2; Macas region, 3.

PERU: Utcuyacu, 4800 ft., 1; Chilpes, 7300 ft., 1; Tulumayo, 4000 ft., 1; Torontoy, 7800 ft., 3; San Miguel Bdg., 5000 ft., 1; Rio Inambari, 2200 ft., 1; Santo Domingo, 6000 ft., 2.

##### **Buarremon inornatus.**

ECUADOR: Pallatanga, 4200–5000 ft., 5; Junction Chimbo-Coco, 2800 ft., 2; Porvenir, 1; Junction Chanchan and Chiguancay Rivers, 2500 ft., 3; Pagma Forest, 6200 ft., 1; 7200 ft., 2; "Jima" (see antea), 1.

##### **Buarremon assimilis assimilis.**

ECUADOR: Pichincha, 4; Yanacocha, 11000 ft., n. w. slope Pichincha, 1; Verda-cocha, n. w. slope Pichincha, 4; Nono, 1.

COLOMBIA: Andes w. of Popayan, 10340 ft., 3; Laguneta, 6; Sta. Isabel, 1; El Piñon (above Fusugasugá), 1.

##### **Buarremon assimilis nigrifrons.**

ECUADOR: Alamor, 4550 ft., 10; Guaniche, 3200 ft., s. e. of Alamor, 3; Guachanomá, 9050 ft., 1; Cebollal, 3100 ft., Pacific slope, w. of Alamor, 1; Las Piñas, 3600 ft., Alamor Mts., 2; La Puente, 2500 ft., w. of Sta. Rosa, 1; Punta Sta. Ana, Portovelo-Loja Trail, 4000 ft., 3; Loja, 2; Salvias, Zaruma-Zaguaro Trail, 6600 ft., 2; Portovelo, 2700 ft., 9; above Zaruma, 6000 ft., 5.

PERU: Palambla 6 ♂.

##### **Buarremon assimilis costaricensis.**

COSTA RICA: Boruca, 3.

##### **Buarremon atricapillus atricapillus.**

COLOMBIA: no locality, the type; La Frijolera, 5000 ft., Cen. Andes, 2; Mts. near Honda, 1.

##### **Buarremon atricapillus tacarcunæ.**

PANAMA: Tacarcuna, 4.



**Buarremon poliophrys.**

PERU: Maraynioc, 1 ♂.

**Buarremon torquatus.**

BOLIVIA: Yungas, 3600 ft., 2 ♂; Incachaca, 7700 ft., 6 ♂, 3 ♀.

**Buarremon fimbriatus.**

BOLIVIA: Tujma, 8200 ft., 2 ♂, 5 ♀, 1 ?

**Buarremon basilicus.**

COLOMBIA: Santa Marta, Valparaiso, 6 ♂, 3 ♀.

**Buarremon phæopleurus.**

VENEZUELA: Silla de Caracas, 1 ♂.

**Buarremon phygas.**

VENEZUELA: Guácharo, 1 ♀.



PLATES XIV TO XVII



PLATE XIV

Mutation in *Buarremon brunneinuchus*

*a.*—*Buarremon brunneinuchus*, Amer. Mus. No. 122824; Buena Vista, above Villavicencio, Eastern Andes, Colombia.

*b.*—*Buarremon inornatus*, Amer. Mus. No. 173587; junction Rios Chimbo and Coco, Ecuador.

*c.*—*Buarremon brunneinuchus*, Amer. Mus. No. 118183, Ricuarte, southwest Colombia. To show variability in pectoral band; an approach toward *B. inornatus*.

*d.*—*Buarremon inornatus*, Amer. Mus. No. 173584; Los Llanos, near Pallatanga, Ecuador. To show indication of pectoral band.







PLATE XV

Mutation in *Buarremon assimilis*

*a.*—*Buarremon assimilis*, Amer. Mus. No. 109376; Laguneta, Central Andes, Colombia.

*b.*—*Buarremon poliophrys*, Amer. Mus. No. 170069; Maraynioc, eastern Peru.

*c.*—*Buarremon assimilis*, Amer. Mus. No. 173089; near Nono, Ecuador. Mutant specimen of *B. assimilis* with pectoral band of *poliophrys*.

*d.*—*Buarremon assimilis*, Amer. Mus. No. 112857; Laguneta, Central Andes, Colombia. Showing indication of pectoral band.







PLATE XVI

Mutation in *Buarremon torquatus*

*a.*—*Buarremon torquatus*, Amer. Mus. No. 138145; Incachaca, Cochabamba, Bolivia.

*b.*—*Buarremon fimbriatus*, Amer. Mus. No. 139750; Tujma, Cochabamba, Bolivia. A mutant form of *torquatus* with fringed pectoral band, and superciliary reaching to the base of the bill.

*c.*—*Buarremon fimbriatus*, Amer. Mus. No. 139756; Tujma, Cochabamba, Bolivia. Showing decrease in size of pectoral band, and consequent approach to *B. borelli*.





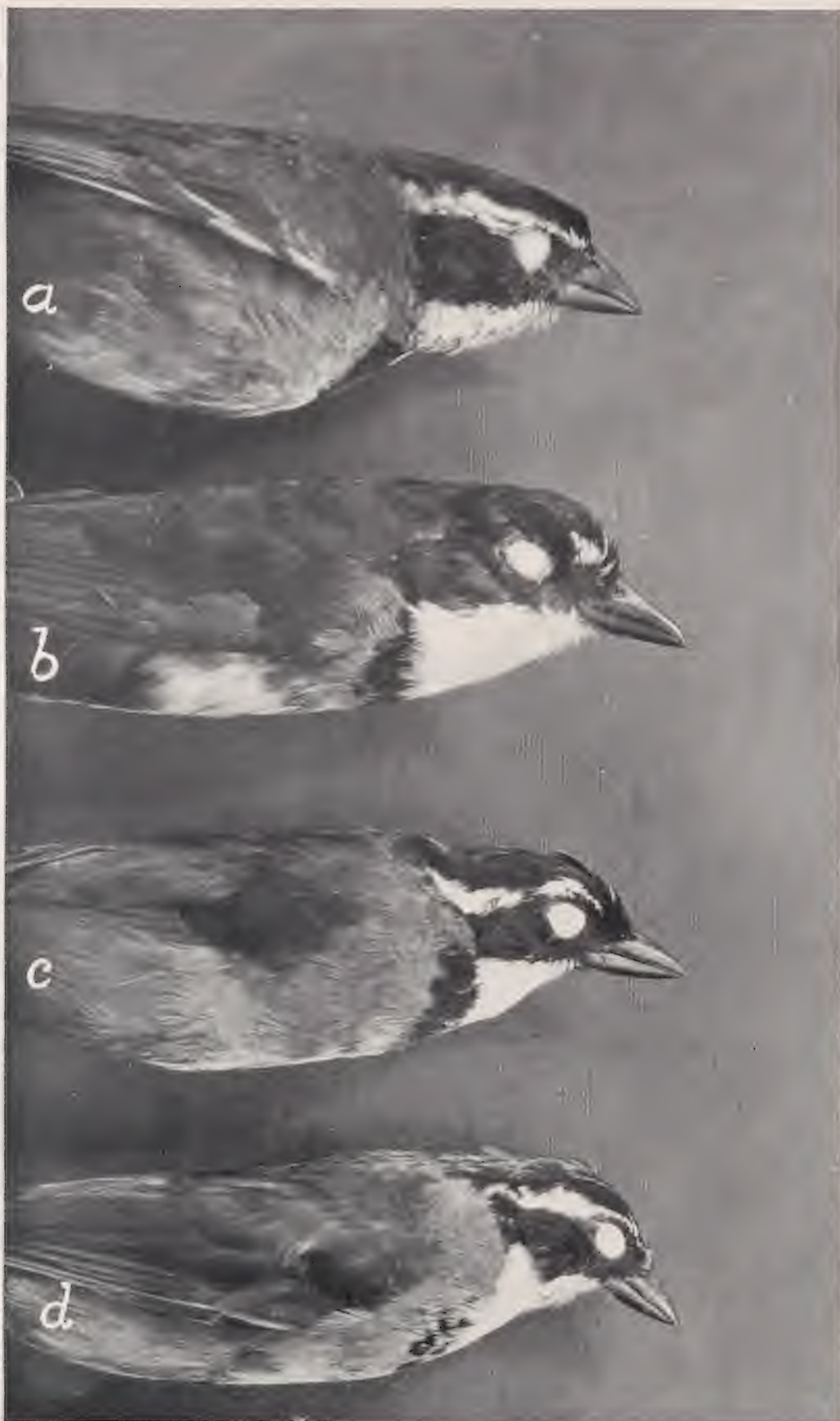


PLATE XVII

Variations in the Superciliary

- a.—Pipilo torquatus torquatus.*
- b.—Buarremon brunneinuchus.*
- c.—Buarremon torquatus.*
- d.—Buarremon fimbriatus*











**Article X.**—THE CARPUS OF *ERYOPS* AND THE STRUCTURE OF THE PRIMITIVE CHIROPTERYGIUM

BY W. K. GREGORY, R. W. MINER AND G. K. NOBLE

The recent papers by Steiner (1921, 1922) and by Huene (1922) have raised again the old question of the structure of the primitive chiropterygium. Since this problem was discussed by the senior writer (Gregory, 1915) some evidence has been brought forward to modify or to supplement the conclusions reached at that time. This evidence has been considered by the present writers while undertaking independent lines of investigation. As it was found that our conclusions agreed, it seemed advisable to publish these conclusions in advance of our other work, which only indirectly considers the structure of the primitive chiropterygium.

The problem is immediately concerned with the phylogenetic significance of the prepollex, prehallux, and postminimus. It is not our intention to discuss the numerous arguments which have been brought forth to support various theories in regard to these elements. Some of these theories are most curious, as for example, the one recently offered by Gillies and Hopkins (1922). The following remarks may be taken as a reply to Gillies and Hopkins, and as a supplement to the views expressed by Steiner and by Huene.

Without attempting a historical sketch, it may be briefly stated that it is now fairly well established that the Tetrapoda arose from crossopterygian ancestors and very probably from some generalized rhipidistian. Investigators such as Wintrebert (1922) who have disputed this conclusion have, for the most part, limited their studies to only a few sets of structures and have not considered all of the numerous characters upon which this conclusion is based.

The two best preserved pectoral limbs found among the Rhipidistia are those of *Sauripterus* and *Eusthenopteron*. A complete description of these limbs has been given by Gregory (1915) and by Bryant (1919). In both genera a single proximal element or humerus articulates with a small coraco-scapula attached to a large cleithrum. Distally, two elements, a radius and an ulna, articulate with the humerus. In *Sauripterus* two radials attach to the radius and two to the ulna, while the latter two form the basis for additional radials. In *Eusthenopteron* the radius does not bear radials and the ulnar series of radials is reduced. It should be noted, however, that the radius is perfectly distinct from the ulna and its series of radials.



The homology of the humerus, radius, and ulna of these crossopterygians with elements of the same name in the Tetrapoda is obvious. The development and musculature of the pectoral appendage of *Polypterus* confirms this homology. Much confusion has arisen by the use of the terms preaxial and postaxial in former discussions. The various adaptations of the ichthyopterygium to locomotion have little bearing on the question of homology. The radius of crossopterygian and tetrapod has a preaxial origin, although in later development it may assume a more postaxial position (e.g., in frogs).

The great difficulty has been to homologize the tetrapod carpus with elements in the crossopterygian limb. It will be recognized at once that the homology cannot be a very exact one. Numerous fusions, losses, or even additions, may have taken place within the carpus. Although the modern tendency in palæontology is to consider that most skull elements do not fuse, but become reduced and finally disappear, we know from the development in modern Amphibia that numerous fusions have taken place within the carpus and tarsus. It therefore would not require a great stretch of our imagination to suppose that the number of radials in the pectoral appendages of *Sauripterus* was reduced by fusion, to a condition such as that found in primitive tetrapods (Fig. 3).

In making the comparisons, it would be well to examine first the structure of the more primitive chiropterygium. The oldest known carpus is that of *Eryops megacephalus*, already described many times (see Gregory, 1915, p. 368). In the best preserved specimen of this carpus (Amer. Mus. No. 4186) there is a gap distal to what has been called "carpal 2." It has been assumed that there was originally a digit, which has been lost in preservation, opposite this carpal. The restored manus would thus have five digits, as figured (Gregory, 1915). It was recognized that no other amphibian, fossil or recent, was known to have five digits in the manus, but the structure of the specimen seemed to indicate that there were originally five in *Eryops*. *A priori*, one would assume that the primitive Amphibia must have had five digits, since there is much evidence to believe that reptiles sprang from the Labyrinthodontia.

Recently, Huene (1922, Fig. 44) has produced a sketch of this same carpus which he states he made over ten years ago from the original. Huene, influenced by the recent work of Steiner, has attempted to make a reconstruction of this carpus, on the assumption that some of the elements in the specimen were pushed out of place before preservation. The reconstruction which Huene has produced did not impress the present



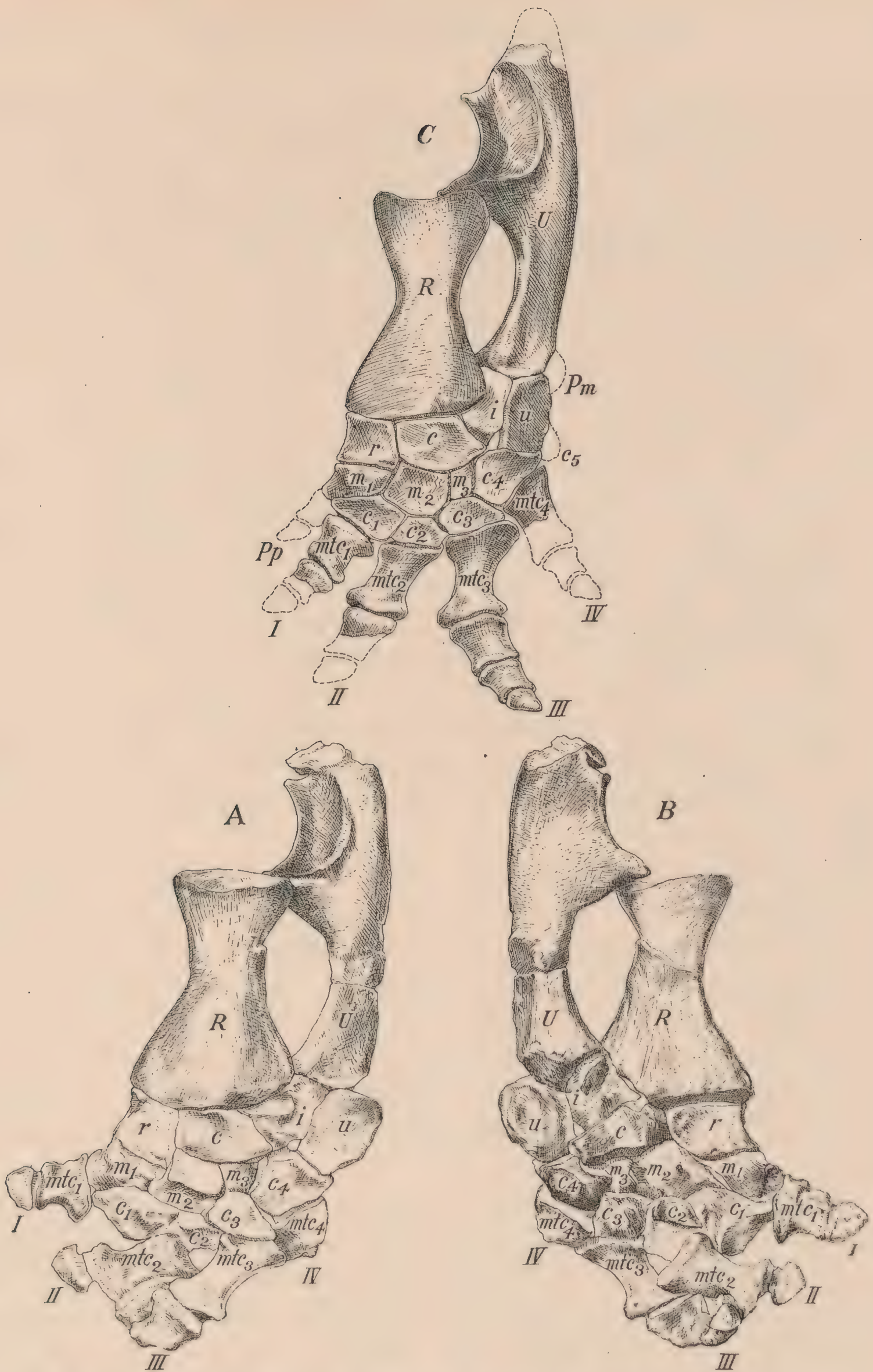


Fig. 1. A, Lower arm, carpus and manus of *Eryops megacephalus*, extensor side (drawn from original specimen, Amer. Mus. No. 4186, one-third natural size).

B, Same, flexor side.

C, Restoration of lower arm, carpus and manus of *Eryops*, based on above specimen (drawn in perspective, one-third natural size).



writers as a very "workable" one. Careful examination of the original carpus has convinced us that Huene is mistaken as to displacement of some of the elements. It has also convinced us that the old reconstruction adopted in the literature is incorrect in several particulars. A correct understanding of these details is necessary before proceeding further with our problem.

It is apparent from the figure of the specimen under discussion (Fig. 1, *A* and *B*) that the carpus as a whole must have withstood a force which dislocated most of the elements slightly toward the radial side. An examination of the articular surfaces of the various carpal elements shows that this dislocation was not great. The large element indicated by Huene as "Ce+5" could not have been originally in the position which Huene indicates in his reconstruction. Its articular surfaces, together with a slight notch on its preaxial side, shows that this element is an ulnare resting in approximately its original position (Fig. 1 *A*, *B*), and not overlapping the intermedium as stated by him (Huene, 1922, p. 455).

Huene, nevertheless, is correct in assuming that the first digit has been displaced. Its articular surface fits exactly on "carpal 2" ( $c_1$  in Fig. 1). Shifting digit I to this position reduces the number of digits by one, and gives *Eryops* only four digits in the manus, similar to all other known Amphibia.

Further examination discloses that the carpus before us has not only undergone a slight preaxial dislocation, but has also been decidedly flattened before fossilization. The articular surfaces of the various carpal elements clearly indicate that the carpus was originally arched—convex above. In the flattening process the articular surfaces of the carpal elements were sprung, and the ulna pushed the intermedium out of place. The intermedium bears a distinct notch (poorly indicated by Huene) which must have received the postaxial, distal corner of the radius on its flexor side.

When the carpal elements are pushed back into position in such a way that their articular surfaces make contact, a compact carpus results, one very similar to the carpus of primitive urodeles. It differs from the urodele carpus in having more elements and in forming a shallow arch.

Restoring the first digit of the manus of *Eryops* before us to its original place exposes a small but undoubted articular surface on the end of the most distal carpal of the first preaxial series. This is too small to have carried the displaced digit found in partial contact with it, and must have originally carried a distal element much smaller than any digit. Comparison of the carpus with that of several of the more generalized



salamanders (hynobiids), or even with the carpus of some advanced types (*Ambystoma opacum*, Fig. 2 A), has led us to believe that this element must have been a prepollex.

There can be no doubt that the prepollex is a primitive structure. Its presence in the most generalized urodeles and its almost universal occurrence in the Salientia confirms this opinion.

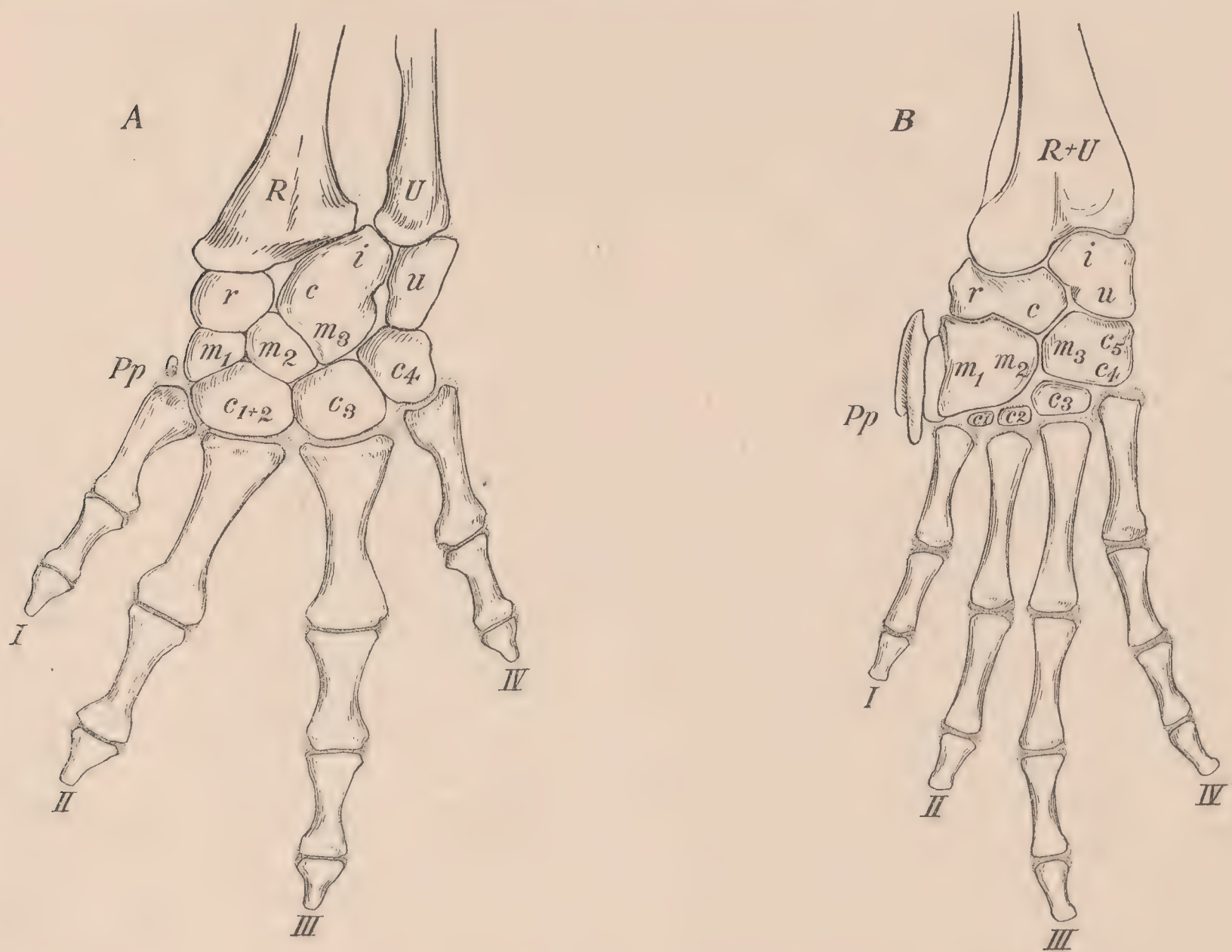


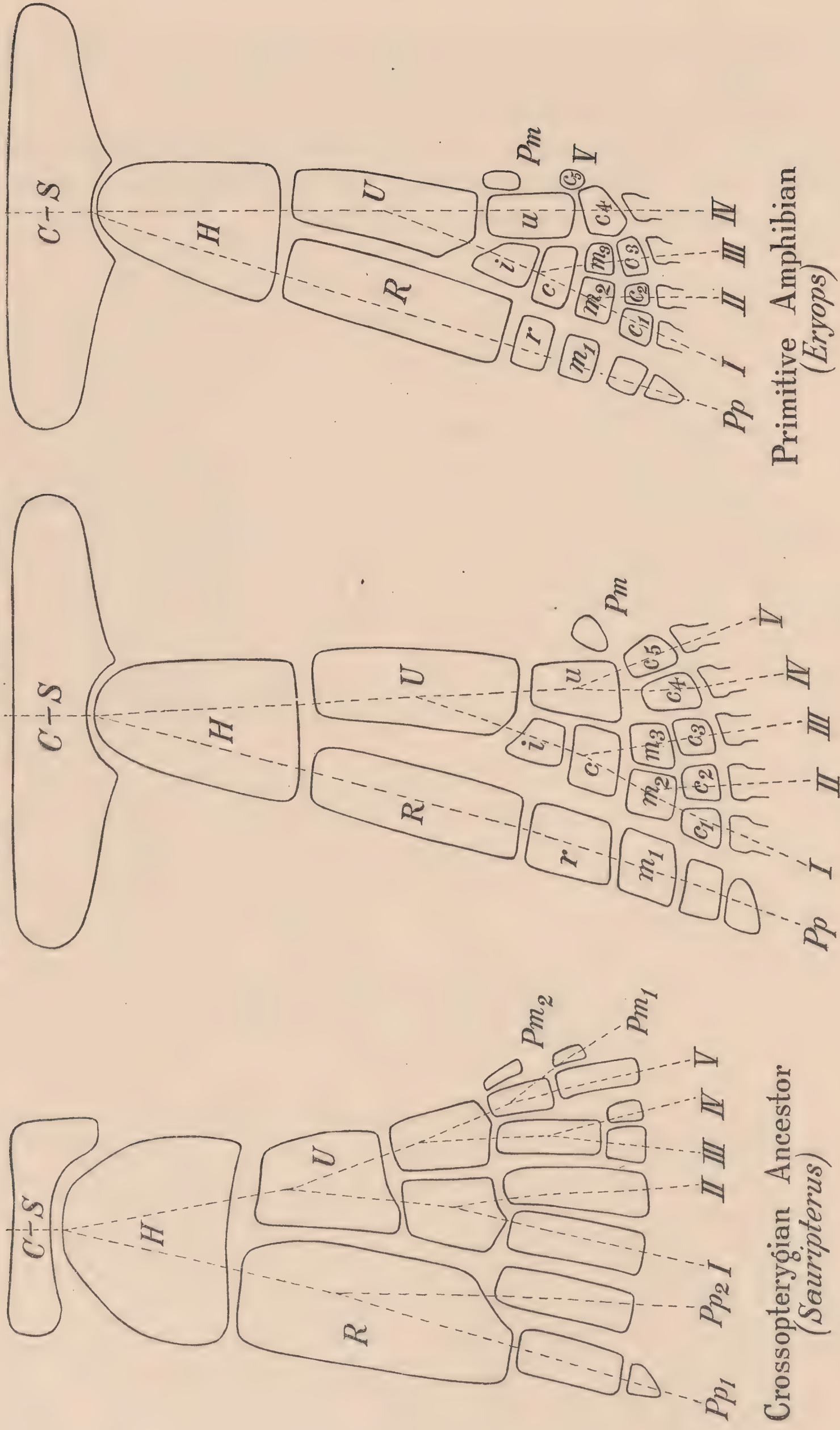
Fig. 2. Carpus of modern Amphibia.  
A, *Ambystoma opacum* (Gravenhorst).  
B, *Ascaphus truei* Stejneger.

The carpus of *Eryops*, then, consisted of a radial series (Fig. 3), ending in a prepollex, and an ulnar series carrying the four digits. This distinction between the radial and ulnar series, although emphasized long ago (Emery, 1894, 1898), has been often confused since, and we are largely indebted to Steiner (1921, 1922) for the clear way in which he has reviewed the whole subject, and pointed out this distinction.

Steiner, however, has not given a complete account and, both for reasons of priority and for simplicity, we have adopted names other than those employed by him for the medium transverse series of carpal elements. Schmalhausen (1917) has compared this median series with



# Evolution of the Carpus



Crossopterygian Ancestor  
*(Sauripterus)*

Ancestral Tetrapod  
*(Hypothetical - based on Bombina Larva)*

Primitive Amphibian  
*(Eryops)*



the median elements in the tarsus of *Ranodon sibericus*, and his term, "mediale," for the elements of this series, seems appropriate. The term mediale is merely indicative of position. As shown in Fig. 3,  $m_1$  belongs to the radial series,  $m_2$  and  $m_3$  to the ulnar group.

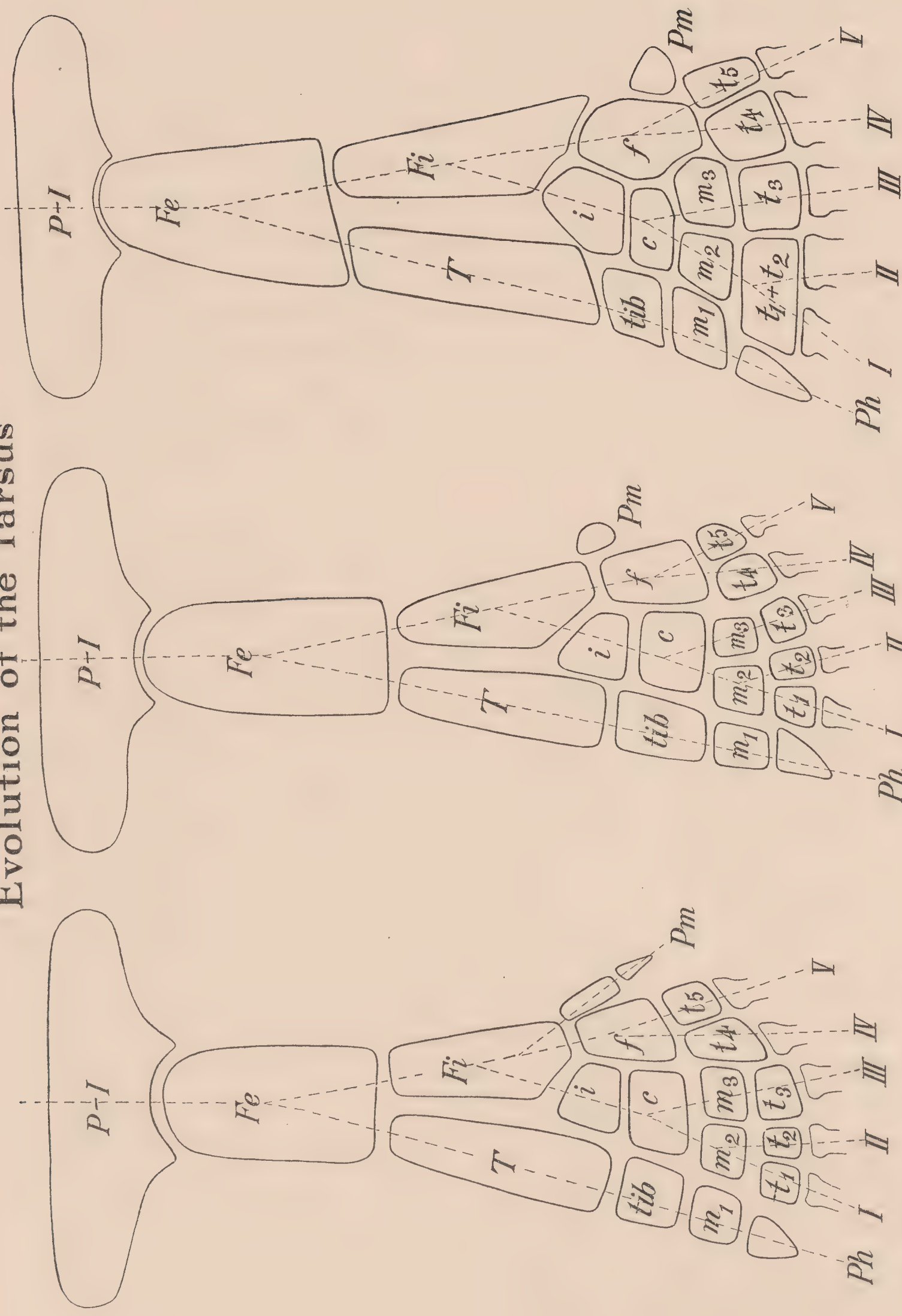
It will be noted that our reconstruction of the manus of *Eryops* (Fig. 1C) is practically identical with the primordial chiropterygium postulated by Steiner (1922, Fig. 13), except for the absence of the fifth digit and its carpal. This primitive chiropterygium possessed a prepollex at the termination of a radial series, and five digits terminating the ulnar series. There was also some indication of a postminimus or sixth digit. The primitive tetrapod carpus exhibited three medalia and one centrale in addition to the proximal r, i and u, and the distal  $c_1$ - $c_5$ . The carpus of all Amphibia, fossil or recent, has become specialized in the loss of the fifth digit (or its reduction to a small cartilage) and in the loss of the postminimus or the sixth digit.

What evidence is there that the Amphibia ever possessed a fifth finger? The evidence is chiefly embryological and as that has been fully discussed by Steiner (1921, 1922), it need not be repeated here. In the embryos of both urodeles and frogs the fifth finger is clearly marked out in blastoderm but never differentiates. The primitive reptiles need not have developed their pentadactyl fore limb from a typical amphibian limb by addition—say by mutation—of a fifth finger, but both reptiles and amphibians probably evolved from pentadactyl ancestors. These ancestors were, of course, Amphibia and probably Embolomeri. Very early in their phylogeny the Amphibia lost the outer finger and its carpal. The foot (Fig. 4), however, being more conservative, retained its original form in some of the Rhachitomi (*Trematops*) and underwent only very few fusions in the more primitive urodeles (Schmalhausen, 1917; Steiner, 1921). The carpus of recent Amphibia has specialized by additional fusions. In the Salientia, because of the narrow and twisted wrist, this specialization is extreme. The embryo and even the adult carpus of such a primitive form as *Ascapbus* (Fig. 2 B) suggests where these fusions have occurred.

It should also be pointed out that Haughton has recently found in *Rhinesuchus*, a close relative of *Eryops*, that there were only four digits in the manus. Unfortunately, the carpus of Haughton's specimen was not well preserved and our knowledge of the carpus of these primitive Rhachitomi rests chiefly upon the evidence furnished by the well-preserved manus of *Eryops* described above.



# Evolution of the Tarsus



Ancestral Tetrapod  
 (Hypothetical - based on *Ambystoma* Larva)  
 Primitive Amphibian  
 (*Trematops*)  
 Recent Urodele  
 (Primitive *Hynobid* - *Ambystomid* type)



The modifications of the carpus and tarsus throughout the vertebrate series have recently been reviewed by Steiner (1921, 1922) and need not be entered into here. It may be mentioned that the distinction between radial carpus and ulnar carpus is an important one; and, while the prepollex is sometimes lost, the distinction is still clear. This is especially noticeable in the musculature of this region. The definitive musculature of the digits converges to the ulna, while the radial musculature is primarily associated with the radial series of carpal elements. As these features will be discussed in a later paper by one of us, they need not be further mentioned here.

It may be pointed out, however, that some of the details of Steiner's work cannot be accepted. Thus, the phalangeal formula of 2-2-3-4-2 is not characteristic of the tarsus of *Ambystoma*, but of only a small group of species of that genus. The Hynobiidæ are certainly more primitive than the Ambystomidæ and may be ancestral to them. Further, all hynobiids and many ambystomids, possessing five toes, have a phalangeal formula of 2-2-3-3-2. Thus, it would seem that the extra phalanx in the fourth toe of the *tigrinum* group of ambystomas may be either a progressive (as in the first finger of some gekkos), or possibly an atavistic mutation (since most branchiosaurs possess a phalangeal formula of 2-2-3-4-3).

The phalangeal formula in the manus of *Eryops* could not have been as high as that usually given in the literature. A careful examination of the original specimen shows that there is no evidence of there being more than 2-2-3-2 phalanges. It is this number which we have indicated in our reconstruction (Fig. 1 C). It will be noted that this formula is the same as that found in primitive salamanders. Frogs and some branchiosaurs have one more phalanx in the fourth digit.

#### SUMMARY

(1) *Eryops* had only four digits in the manus.

(2) *Eryops* possessed a well-developed prepollex.

(3) The carpus (as well as the tarsus) consists of two moieties; the radius (tibia) moiety, embracing the prepollex (prehallux) and carpal elements, forming the first preaxial ray, and the ulna (fibula) moiety, including the digits and their carpals, converging toward the ulna (fibula). The distinctness of these two moieties is further demonstrated by the subdivisions of the carpal (or tarsal) musculature.

(4) The pectoral appendage of *Eryops* is readily comparable with the pectoral fin of the rhipidistian crossopterygians. The distinctness of the two primary series of carpal elements even in these forms is obvious.



(5) All known Amphibia, recent and fossil, possess only four digits in the manus, but embryological and indirect palæontological evidence allows us to infer that the most primitive Amphibia had a prepollex, five digits, and a postminimus in the hand; a prehallux, five digits, and a postminimus in the foot.

(6) The primitive chiropterygium was therefore at least seven-rayed in both the manus and pes, but with a tendency toward a reduction in the two marginal rays, which has proceeded furthest in the last postaxial ray.

(7) The carpus of *Eryops* and the primitive chiropterygium possessed three medalia and one centrale, as well as the radiale, intermedium, ulnare and carpalia.

(8) The phalangeal formula of *Eryops* was only 2-2-3-2 in the manus.

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# Article **XI.**—CLASSIFICATION OF THE LIZARDS

BY CHARLES LEWIS CAMP

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INTRODUCTION

The present paper is an attempt to define more fully the structural relationships of the Sauria. The views here expressed are the result of a correlation of previous investigation with certain efforts of my own touching upon morphology and paleontology, and the effort is made to furnish a more perfect historical and taxonomic picture, which, it is hoped, will aid studies and emphasize in outline certain developmental tendencies in a group which seems to be almost unequalled in the interesting number of convergent and parallel forms it comprises.

I have recently undertaken to determine the range of variation of the muscular system in the lizards and hope to publish the results of this work. Findings in myology thought to be of value in a taxonomic sense are included in the present paper.

After examination of the muscles of almost all parts of the body among representative adaptive and taxonomic types some features of the superficial body and throat musculature are believed to be indicative of relationship. The throat region exhibits complex "patterns" developed similarly in most of the superfamilies. These patterns result from an interdigitation of differently directed layers and bundles. In general, the style of the pattern cannot be considered as adaptive, though the size of various bundles comprising the pattern, their insertion on skin, mid-ventral raphe or hyoid, may be very directly so.

In addition, a series of thirty-odd characters has been selected, and a check made of the distribution of each among the families of the sub-order.

The material has been obtained mainly from the collections of the Department of Herpetology of the American Museum and my thanks are especially due to Miss Mary C. Dickerson, Dr. G. K. Noble, and Mr. Karl P. Schmidt for their generous interest, valuable counsel and the loan of important specimens for dissection.

Furthermore, Dr. Noble has permitted the use of a series of carefully cleared specimens including many geckos, a xantusid, an iguanid



and a teiid, which have proven useful in the osteological study of these small forms.

I am indebted to Drs. Thomas Barbour and Joseph Grinnell for loan of specimens from the collections under their charge.

A survey of the paleontological evidence as to the derivation of the Sauria and the history of the sub-groups has been thought indispensable, and this review has been extended by a study of Cretaceous, Eocene and Oligocene material from the collections of the Department of Palæontology of the American Museum and made available for my use through the kindness of Dr. W. D. Matthew and Mr. Walter Granger.

The late Professor Williston's manuscripts and well-known papers have been of the greatest help in allocating fossil genera and determining the nature of supposedly primitive characters among recent lizards.

The present work has been done under the supervision of Dr. W. K. Gregory and is due primarily to his inspiration. The author wishes both to properly acknowledge this and to thank him for his patience and his faithful interest in the slow growth of these results.

It is pleasant to record that the work leading up to the present paper and to other projects now in hand, dealing with the myology and adaptive radiation of the Sauria, has been made possible only through the generous facilities placed at my disposal in The American Museum of Natural History by its president, Professor Henry Fairfield Osborn. And I should also wish to acknowledge with warmest thanks the courtesy of the authorities of the University of California and Miss Annie M. Alexander who have kindly furnished the funds for concluding this research.

Most of the drawings are due to the excellent skill of Mrs. E. L. Beutenmüller. The plates have been lettered by Mr. William Belanske.

#### HISTORY OF SAURIAN CLASSIFICATION

Cope's synopsis of 1864 marked a turning point in knowledge of saurian relationships. Before this time a score of schemes had been proposed based chiefly upon the obvious characters of physiognomy, feet and limbs, tongue, squamation, and habits. The pre-Copeian period is in part reviewed in the first volume of Duméril and Bibron's '*Erpétologie Générale*,' 1834. Early systems which have contributed to present views are those of Brongniart (1800), Duméril (1807), Cuvier (1817), Merrem (1820), Latreille (1825), Gray (1825), Fitzinger (1826), Wagler (1830), Duméril and Bibron (1834-1854), Wiegmann (1834), Gray (1845), and Stannius (1856).



Cope's researches leading up to his first summary of results (1864) involved a consideration of many details of the osteology for the first time examined among lizards. His scheme formed the basis of Boulenger's conservative arrangement (1884) employed in the second edition of the British Museum Catalogue (1885-1887). Cope enlarged the field again in 1892 in a paper that formed the systematic basis of his 'Crocodilians, Lizards and Snakes of North America,' 1900,—a great body of morphological fact, considered from the taxonomic standpoint.

Baur, Boulenger, Fürbringer, Gadow, Williston, Stejneger, and many others cited in the text are well known for important recent contributions.

Boulenger (1884 et seq.) has not employed names for groups of lizards higher than the family. Gill (1886) in a review of Boulenger's system has attempted to supply superfamily divisions based on characters employed by Boulenger. Stejneger (1907) has in part followed the nomenclature of Gill.

The latest views of Cope (1900) are based on his own system of 1864 with modifications. He regards the serpents as related to the amphisbænians, the Xenosauridæ as related to the geckos and the geckos as degraded "in the characters of their vertebræ, for [he does] not believe this character to be of primitive origin." I have taken exception to these views, but I should support his arguments that the chameleons are modified agamids and that the pygopodids are diploglossids.

Cope recognized nine suborders (or superfamilies?) of the Sauria including twenty-four families. Certain ambiguities, for example, the double allocation of the Anniellidæ, make it impossible to determine just what were some of Cope's final opinions. The work (1900), unfortunately, had to be edited and published posthumously. The arrangement was:

|                         |                                  |
|-------------------------|----------------------------------|
| Squamata (Subclass)     | Helodermatoidea                  |
| Ophidia (Order)         | Helodermatidæ                    |
| Pythonomorpha           | Diploglossa                      |
| Sauria                  | Zonuridæ, Pygopodidæ, Anguidæ,   |
| Rhaptoglossa (Suborder) | Xenosauridæ                      |
| Chamæleontidæ           | Leptoglossa                      |
| Pachyglossa             | Teiidæ, Xantusiidæ, Lacertidæ,   |
| Agamidæ, Iguanidæ       | Gerrhosauridæ, Scincidæ, Acon-   |
| Nyctisaura              | tiidæ, Dibamidæ, Anelytropi-     |
| Eublepharidæ, Geckonidæ | dæ                               |
| Uroplatoidea            | Annulati                         |
| Uroplatidæ              | Anniellidæ, Euchirotidæ, Amphis- |
| Thecoglossa             | bænidæ, Trogonophidæ             |
| Varanidæ                |                                  |



Cope regarded his *Pachyglossa* as ancestral to the *Rhaptoglossa*, *Nyctisaura*, and *Diploglossa*, and the latter as giving rise to the *Thecoglossa*, *Leptoglossa* and *Annulati*.

Fürbringer (1900) coincidently with Cope proposes the following scheme:

Order Lacertilia

/ Suborder Lacertilia vera

Gens *Nyctisaura* s. *Geckonomorpha*

Fam. *Geckonidæ*, *Eublepharidæ*

Gens *Pygopodomorpha*

Fam. *Pygopodidæ*

Gens *Leptoglossa* s. *Autosauromorpha*

Superfam. *Scinco-Lacertæ*

Fam. *Scincidæ*, *Anelytropidæ*, *Dibamidæ*, *Gerrhosauridæ*, *Lacertidæ*

Superfam. *Teji*

Fam. *Tejidæ*, *Xantusiidæ*

Gens *Diploglossa* s. *Anguimorpha*

Superfam. *Zonuri*

Fam. *Zonuridæ*

Superfam. *Angues*

Fam. *Anguidæ*

Fam. *Anniellidæ*

Superfam. *Helodermates*

Fam. *Helodermatidæ*

Superfam. *Xenosauri*

Fam. *Xenosauridæ*

Gens *Pachyglossa* s. *Eunota* s. *Iguanomorpha*

Fam. *Telerpetidæ* (uncertain), *Iguanidæ*, *Agamidæ*

Gens *Gecko-Chamæleontes* s. *Uroplatimorpha*

Fam. *Uroplatidæ*

Suborder Platynota s. *Varano-Dolichosauria*

Gens *Varanomorpha*

Fam. *Varanidæ*

Gens *Dolichosauromorpha*

Fam. *Aigialosauridæ*

Fam. *Dolichosauridæ*

Suborder Mosasauria

Gens *Mosasauromorpha*

Fam. *Mosasauridæ*

/ Suborder Amphisbænia

Gens *Amphisbænomorpha*

Fam. *Amphisbænidæ*

“(vielleicht mit den Subfamilien *Chirotinæ*, *Trogonophinæ*, s. *Amphisbænidæ oxyuræ* und *Amphisbæninæ* s. *Amphisbænidæ amblyuræ*).”

/ Suborder Chamæleontia

Gens *Chamæleontomorpha*

Fam. *Chamæleontidæ*



He regards the geckos as primitive. His views are derived chiefly from a study of the shoulder girdle apparatus, and other parts of the anatomy are not extensively considered.

Gadow (1901) reviews the characters employed by Cope and Boulenger and adopts the following system:

Subclass

Pythonomorpha

Order I Dolichosauri

Order II Mosasauri

Subclass

Sauria

Order I Autosauri or Lacertilia

Suborder I Geckones

Geckonidæ (Geckoninæ, Eublepharinæ, Uroplatinæ)

Suborder II Lacertæ

Group I. Agamidæ, Iguanidæ, Xenosauridæ, Zonuridæ, Anguidæ, Helodermatidæ, Lanthanotidæ, Anniellidæ

Group II. Xantusiidæ, Tejidæ, Amphisbænidæ

Group III. Scincidæ, Gerrhosauridæ, Lacertidæ, Anelytropidæ, Dibamidæ (uncertain)

Group IV. Varanidæ

Suborder III Chamæleontes

Chamæleontidæ

Order II Ophidia

Gadow regards the Pygopodidæ as too obscure for a place in the system, the Chamæleontidæ as of unknown origin, the geckos as an independent and very old branch of the saurians, and the Iguanidæ and Anguidæ as closely related in somewhat the way Boulenger (1884) has suggested.

Williston (1904) has outlined a system and has lately (in manuscript) briefly reviewed the characters that support it:

Order Squamata (Lepidosauria)

Suborder Sauria (Lacertilia)

Superfamily Platynota

Family Varanidæ

Dolichosauridæ

Aigialosauridæ

Superfamily Mosasauria

Family Mosasauridæ

Superfamily Kionocrania (true lizards)

Superfamily Amphisbænia

Superfamily Rhiptoglossa

Suborder Serpentes (Ophidia)

Williston's contribution seems especially valuable for its carefully drawn perspective of the relations of the mosasaurs.



## SELECTION OF NAMES

I have in most cases followed suggestions of Stejneger (1907, p. 49) in applying names to groups higher than the superfamily. New names proposed are as follows, fossil groups being indicated by a dagger.

|                         |               |
|-------------------------|---------------|
| Scincomorpha (Section)  | †Megalaninæ   |
| †Ardeosauridæ           | †Saniwinæ     |
| Feyliniidæ <sup>1</sup> | Zonurinæ      |
| Anelytropsidæ           | Chamæosaurinæ |
| Varaninæ <sup>2</sup>   |               |

Groups recharacterized and placed under old names or emended names are:

|                           |                                 |
|---------------------------|---------------------------------|
| Ascalabota (Division)     | Autarchoglossa (Division) Cont. |
| Gekkota (Section)         | †Euposauridæ                    |
| Iguania (Section)         | Platynota (Subsection)          |
| Autarchoglossa (Division) | Diploglossa (Subsection)        |
| Xantusioidea              | Pygopodoidea                    |
| Scincoidea                | Anguioidea                      |
| Lacertoidea               | †Glyptosauridæ                  |
| Anguimorpha (Section)     | Zonuroidea                      |

First usage of the names employed is indicated in the following list.

## Suborder Sauria

1802—MacCartney, in Ross' 'Transl. Cuvier's Lect. Comp. Anat.,' I, tab. III. [cf. Gill, 1900].

## Division Ascalabota

1820—Merrem, 'Tentamen Syst. Amphib.,' p. 9 (*Ascalabotæ*).

## Section Gekkota

1825—Latreille, 'Fam. Nat. du Règne Animal,' p. 96 (*Geckotii*).

## Section Iguania

1825—Latreille, *loc. cit.*, p. 95 (*Iguanii*).

## Section Rhiptoglossa

1834—Wiegmann, 'Herp. Mex.,' p. 6 (*Rhiptoglossa*)

<sup>1</sup>The Feyliniidæ replaces the Anelytropidæ named for *Anelytrops* preoccupied (cf. Boulenger, 1887, p. 431). The Anelytropsidæ includes only the genus *Anelytropsis*.

<sup>2</sup>The Varanidæ I consider as covering the fossil and recent species placed in the genus *Varanus* by Fejérváry (1918). The Megalaninæ is substituted for the Megalanidæ of Fejérváry (*loc. cit.*). The Saniwinæ is proposed for the North American Eocene genera *Saniwa* Leidy and *Thinosaurus* Marsh.



## Division Autarchoglossa

- 1830—Wagler, 'Nat. Syst. der Amphibien,' p. 152  
(Autarchoglossa; omits *Heloderma* and *Varanus*)

## Section Scincomorpha, new name

- (=Leptoglossa Cope, Proc. U. S. Nat. Mus., 1900, p. 201 (*nec*  
Wiegmann, *loc. cit.*), omits Annulata.)

## Section Anguimorpha

- 1900—Fürbringer, Jenaische Zeitschrift, XXXIV, p. 621 (Diploglossa s.  
Anguimorpha, omits Platynota and Mosasauria).

## Subsection Platynota

- 1836—Duméril and Bibron, 'Erpétologie Gén.,' III, p. 437 (Platynotes,  
includes *Heloderma*).  
1890—Baur, Science, November 7, 1890 (Platynota, includes *Helo-*  
*dermatoidea*).

## Subsection Diploglossa

- 1864—Cope, Proc. Acad. Nat. Sci., Phila., XVI, p. 227.

## OUTLINE OF CLASSIFICATION ADOPTED

Suborder **SERPENTES**Suborder **SAURIA**Division **Ascalabota**

## Section GEKKOTA

- †Family Ardeosauridæ
- Family Gekkonidæ
- Family Uroplatidæ

## Section IGUANIA

- Family Iguanidæ
- Family Agamidæ

## Section RHIPTOGLOSSA

- Family Chamæleontidæ

Division **Autarchoglossa**

## Section SCINCOMORPHA

## Superfamily Xantusioidea

- Family Xantusiidæ

## Superfamily Scincoidea

- Family Scincidæ
- Family Anelytropsidæ
- Family Feyliniidæ
- Family Dibamidæ



- Superfamily Lacertoidea
  - Family Gerrhosauridæ
  - Family Lacertidæ
  - Family Teiidæ
- Superfamily Amphisbænoidea
  - Family Amphisbænidæ
- Section ANGUIMORPHA
  - †Family Euposauridæ
- Subsection Platynota
  - Superfamily Varanoidea
    - Family Varanidæ
      - †Subfamily Saniwinæ
      - †Subfamily Megalaninæ
    - †Family Dolichosauridæ
    - †Family Aigialosauridæ
  - Superfamily Mosasauroidea
    - †Family Mosasauridæ
- Subsection Diploglossa
  - Superfamily Pygopodoidea
    - Family Pygopodidæ
  - Superfamily Anguioidea
    - †Family Glyptosauridæ
    - Family Helodermatidæ
    - Family Anguidæ
    - Family Xenosauridæ
    - Family Anniellidæ
  - Superfamily Zonuroidea
    - Family Zonuridæ
      - Subfamily Zonurinæ
      - Subfamily Chamæosaurinæ

#### SYNOPSIS OF CHARACTERS

- I. Rectus superficialis rarely present; usually more than four transverse rows of ventral scales over each body segment; scales with wide free margin ("deciduous"), when imbricate; hemipenes calyculate. . . . Division ASCALABOTA.
  - A. Vertebræ amphicœlous; or procœlous with small condyles and persistent intercentra; centra short, equal in width at both ends and constricted medially; tongue fleshy and non-extensile; postorbital arch incomplete or absent; six cervical vertebræ; Mylohyoideus anterior in a single layer. . . . . Section GEKKOTA.
    - 1. Skull arches absent; clavicle usually more or less expanded and often perforate, or with appearance of having been perforate; interclavicle rhomboid, cruciform, or reduced to a longitudinal bar; nasals separate; body muscles well-developed; Rectus abdominis extensive; Mylohyoideus strong and not overlapped by Constrictor colli. . . . . GEKKONIDÆ.



2. Skull arches absent; clavicle simple; interclavicle minute; nasals fused; body muscles greatly reduced; Rectus abdominis limited; Mylohyoideus weak and largely overlapped by Constrictor colli.

## UROPLATIDÆ.

- B. Vertebrae always procœlous with large condyles and no intercentra; centra short, conical; tongue fleshy and non-extensile; skull arches complete; six cervical vertebrae; Mylohyoideus anterior usually in two layers.

## Section IGUANIA.

3. Dentition pleuro-homodont; Mylohyoideus anterior usually with posteriorly directed superficial portion, with transverse or anteriorly directed principal portion, and no profound portion...IGUANIDÆ.  
4. Dentition hyper-acrodont, usually heterodont; Mylohyoideus anterior with anteriorly directed or transverse principal portion, with posteriorly directed profound portion, and no superficial bundle.

## AGAMIDÆ.

- C. Vertebrae always procœlous with large condyles and no intercentra; centra elongate, cylindrical; tongue vermiform and extensile; skull arches complete; three cervical vertebrae; Mylohyoideus anterior in two layers, arranged as in the Agamidæ.....Section RHIPTOGLOSSA.

5. Nasal bones not bounding nasal apertures; epipterygoid absent, clavicles rudimentary or absent; interclavicle absent; feet zygodactylous, grasping; body muscles weak; Rectus abdominis reduced.....CHAMÆLEONTIDÆ.

- II. Rectus superficialis always present; less than four transverse rows of ventral scales to each body segment; scales with narrow free margin when imbricate; hemipenes usually flounced or plicate.....Division AUTARCHOGLOSSA.

- D. Tongue scaly or with oblique plicæ; hemipenes usually laminate; clavicles, when present, usually dilated, often perforate, and sometimes hook-shaped; interclavicle, when present, usually cruciform; osteoderms, when present, compound on the ventral surface of the body; tooth replacement usually directly successive by intrusion of new tooth into hollow base of old; teeth rarely conical and recurved; caudal chevrons, when present, always intercentral or slightly post-intercentral.

## Section SCINCOMORPHA.

6. Vertebrae of primitive procœlous type as in procœlous geckos; intercentra persistent as small scale-like elements; Rectus lateralis closely attached to belly scales; dorsal scales granular; ventral scales usually squarish, non-imbricate; femoral pores present; no parasternum.....XANTUSIOIDEA.

- (a.) Osteoderms absent on body; supra-temporal fenestra closed by union of squamosal and parietal bones; Mylohyoideus without superficial anterior bundle.....XANTUSIIDÆ.

7. Vertebrae of normal procœlous type with large condyles and tapering centra; no intercentra; Rectus lateralis usually not closely attached to belly scales; scales, imbricate, cycloid, or cycloid-hexagonal; no femoral pores; rudiments, at least, of a parasternum.

## SCINCOIDEA.



- (b.) Skull arches always present; pectoral girdle complete; premaxillaries usually not fused; Mylohyoideus with a superficial anterior bundle; osteoderms present. . . . . SCINCIDÆ.
- (c.) No skull arches; caudal chevrons present (?); no traces of a pectoral girdle<sup>1</sup>; premaxillary single (?); osteoderms present; interorbital septum and epipterygoids present (?).  
ANELYTROPSIDÆ.
- (d.) No skull arches; caudal chevrons present; rudiments of a pectoral girdle; premaxillary single; osteoderms present; interorbital septum and epipterygoids present; Mylohyoideus without anterior superficial bundle. . . . . FEYLINIIDÆ.
- (e.) No skull arches; no caudal chevrons; rudiments of a pectoral girdle; premaxillary double; no osteoderms; no interorbital septum or epipterygoids; Mylohyoideus with anterior superficial bundle. . . . . DIBAMIDÆ.
8. Vertebrae of normal procœlous type with large condyles and tapering centra; no intercentra; Rectus lateralis attached closely to belly scales; dorsal scales granular or imbricate; ventral scales usually squarish and non-imbricate; femoral pores present; parasternum rarely present. . . . . LACERTOIDEA.
- (f.) Osteoderms present; supratemporal fossa roofed over; Mylohyoideus with an anterior superficial bundle.  
GERRHOSAURIDÆ.
- (g.) Osteoderms absent; supratemporal fossa roofed over; Mylohyoideus with an anterior superficial bundle. . . . LACERTIDÆ.
- (h.) Osteoderms absent; supratemporal fossa open; Mylohyoideus without anterior superficial bundle. . . . . TEIIDÆ.
9. Vertebrae with broad flat centra and wide condyles, no neural spines; no intercentra; Rectus lateralis attached closely to belly scales; dorsal scales granular when present; body usually without scales; no parasternum. . . . . AMPHISBÆNOIDEA.
- (i.) Osteoderms absent; no skull arches; no interorbital septum; no epipterygoids; pre-maxillary single; extra-columella enormous. . . . . AMPHISBÆNIDÆ.
- E. Tongue smooth or papillate; hemipenes flounced; clavicles simple; osteoderms, when present, simple, and often corresponding in extent with the horny scales; tooth replacement usually alternate; teeth frequently conical, pointed and recurved; caudal chevrons often attached centrally.  
Section ANGUIMORPHA.
10. Vertebrae highly developed, procœlous, with short, constricted centra; condyles very large and with a flange; seven or more cervical vertebrae; nasals elongate, fused; premaxillaries elongate; lower jaw with a median transverse sutural joint; caudal chevrons pediculate and articulated to the median portion of each centrum; no osteoderms; scales granular; no parasternum.  
Subsection PLATYNOTA.

<sup>1</sup>Fide, Cope, 1892a: I have not seen representatives of this family.



- (j.) Centra depressed; articular surface of condylar ball directed dorsally; digits with claws and without hyperphalangy; a sacrum.....VARANOIDEA.  
 (1) Propodials normal; teeth subpleurodont; seven cervical vertebræ; interclavicle anchor-shaped.  
 VARANIDÆ.  
 (a) A more marked constriction in the centra; no zygosphenal articulation.....VARANINÆ.  
 (b) An exaggerated constriction in the very short centra; a zygosphenal articulation.  
 †MEGALANINÆ.  
 (c) A less marked constriction in the more elongate centra; with or without zygosphenal articulation.....†SANIWINÆ.  
 (2) Propodials shortened; teeth subthecodont; seven cervical vertebræ; interclavicle anchor-shaped.  
 †AIGIALOSAURIDÆ.  
 (3) Propodials shortened; thirteen cervical vertebræ; clavicles and interclavicle reduced or absent.  
 †DOLICHOSAURIDÆ.  
 (k.) Centra cylindrical, condyles directed posteriorly; limbs paddle-shaped; digits without claws and with hyperphalangy; no sacrum.....†MOSASAUROIDEA.  
 (4) Clavicles and interclavicle reduced or absent; teeth subthecodont; seven cervical vertebræ...†MOSASAURIDE.  
 11. Vertebræ of normal procœlous type; centra not constricted in front of condyles; no condylar flange; six cervical vertebræ; nasals normal, separate; premaxillaries normal; lower jaw without sutural joint; caudal chevrons usually not pediculate and when central usually fused with the centrum; osteoderms frequently present; scales usually imbricate; a parasternum in the Chamæosaurinæ.  
 Subsection DIPLOGLOSSA.  
 (l.) Vertebral centra short, cylindrical, slightly constricted medially; condyles almost as wide as the centra; ribs with a long ventral muscular process; preanal pores; no Geniomyoideus; no Mylohyoideus anterior superficialis....PYGOPODOIDEA.  
 (5) Skull arches both lacking; pleurodont; only three or four bones in mandible; no osteoderms..PYGOPODIDÆ.  
 (m.) Vertebral centra tapering, not constricted; condyles never as wide as the centra; ribs sometimes with a dorsal muscular process; no femoral or preanal pores; a Geniomyoideus muscle; a Mylohyoideus anterior superficialis; tooth replacement alternate.....ANGUIOIDEA.  
 (6) Skull arches both present; pleurodont or subpleurodont; six bones in mandible; osteoderms present, non-tuberculate; interclavicle cruciform or transverse; an interorbital septum.....ANGUIDÆ.



- (7) Skull arches both absent; subpleurodont; five bones in mandible; osteoderms present, non-tuberculate; no interclavicle or sternum; no interorbital septum.  
ANNIELLIDÆ.
- (8) Skull arches both present; pleurodont; six bones in mandible; osteoderms present over skull, ornamented with minute tubercles; interclavicle anchor-shaped; an interorbital septum . . . . . XENOSAURIDÆ.
- (9) Skull arches both present; pleurodont; six bones in mandible; osteoderms present over skull and body, imbricate and simple as in Anguidæ but with many minute tubercles. . . . . †GLYPTOSAURIDÆ.
- (10) Postorbital arch present; supratemporal arch absent; subpleurodont; osteoderms present, non-imbricate, nodular, and slightly tuberculate; interclavicle a longitudinal splint; an interorbital septum.  
HELODERMATIDÆ.
- (n.) Vertebral centra tapering, not constricted; condyles never as wide as the centra; ribs without muscular processes; femoral or preanal pores present; no Geniomyoideus muscle; no Mylohyoideus anterior superficialis; tooth replacement successive. . . . . ZONUROIDÆ.
- (11) Skull arches both present; dentition pleurodont.  
ZONURIDÆ.
- (d). Body and limbs normal; osteoderms and zygosphenes sometimes present; two rows of ventral scales over each body segment; no parasternum.  
ZONURINÆ.
- (e). Body serpentiform; limbs reduced; no osteoderms; no zygosphenes; one row of ventral scales over each body segment; a large parasternum. . . . . CHAMÆSAURINÆ.

## REVIEW OF TAXONOMY AND PALEONTOLOGY

### Suborder **SERPENTES**

Brain-case completely bony anteriorly; rami of lower jaw never united by suture; no urinary bladder (Cope, 1900); no pectoral girdle; elements of lower jaw reduced; usually one dorsal temporal element articulating with the quadrate.

In totality of characters the serpents approach the anguimorphine lizards (p. 359). The hemipenes have a similar texture; the brain-case is bony beneath the frontals in *Varanus* and *Heloderma*; the vertebræ of the Varanoidea are similar in shape (cf. Figs. 25, 26) to those of *Python* and sometimes develop a zygosphenes and zygantrum as in the serpents (pp. 322 and 345); the caudal chevrons are universally central in position



in the Platynota and the snakes; in some limbless Diploglossa (p. 376) they are anchylosed to the centra in the same way as in the serpents. The number of transverse ventral scale rows (p. 400) corresponds to the body segments, there being in the Typhlopidae, Glauconiidae, Leptotyphlopidae, and Uropeltidae, as in the saurian Autarchoglossa, two rows to every segment. In all other serpents there is only a single ventral scale for each pair of ribs.

The throat muscles of *Typhlops congestus* (cf. Fig. 53) show typical saurian arrangements, there being a considerable interdigitation of the Geniohyoideus with the Mylohyoideus anterior; a reflected anterior superficial bundle of the Mylohyoideus anterior as in many autarchoglossid lizards; and a very typically placed Cervicomandibularis. All these features are absent in *Sphenodon* and apparently in the Chelonia and crocodiles and the second is unknown in most of the Ascalabota. I am inclined to think the anterior mandibular (Intermaxillaris) muscle is the same as what I have called the Geniomyoideus of the Diploglossa (p. 373).

Maurer (1896) states that the Transversus abdominis is absent in the serpents. I have found it, however, in *Typhlops* and in *Diadophis*.

A tabulare is present in most ophidians but is absent in the Typhlopidae, Glauconiidae, and Uropeltidae.

Ophidian remains are not known from formations earlier than the Cretaceous and are fairly common in the Eocene.

### Suborder SAURIA

Brain-case never completely bony anteriorly; rami of lower jaw usually united by suture; a urinary bladder; not more than two sacral vertebræ, no sacral ribs (Moodie, 1907); usually an ectepicondylar, never an entepicondylar foramen (Williston, 1914); pectoral girdle usually present; articular and prearticular always fused; quadrate streptostylic; usually two dorsal temporal elements articulating with the quadrate.

Fossil reptiles referred by Williston, Nopcsa (1908), and others to the Sauria, but otherwise *incertæ sedis*, occur in the Upper Jurassic<sup>1</sup> (*Saurillus* Owen, 1885,—vertebræ procœlous, dermal scutes present, Lydekker, 1888); Upper Cretaceous (*Coniasaurus* Owen, cf. Nopcsa,

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<sup>1</sup>Under the name *Eifelosaurus triadicus*, Jaekel (1904) has described and figured a reptile with lizard-like habitus from the Triassic. This is apparently a terrestrial form with amphicoelous vertebræ, weakly double-headed ribs, short, stout, curved femora, short, broad, body and broad tail. Parasternal ribs are present. There is no skull and an allocation with the Sauria is problematical (cf. von Huene, 1910a).



provisionally placed with the Dolichosaurs; *Saurospondylus* Seeley, referred by Woodward and Sherborn to the genus *Dolichosaurus*,—an allocation questioned by Nopcsa; *Tylosteus* Cope, cf. Hay 1901, p. 477); Eocene (*Enigmatorosaurus* Nopcsa [for *Thaumastosaurus* de Stefano, 1903, preoccupied], *Naocephalus* Cope, cf. Nopcsa); and Pleistocene (*Notiosaurus* Owen, *Patricosaurus*, Seeley, cf. Nopcsa).

#### Division **ASCALABOTA**

The geckos, iguanoids, and chameleons are distinguished by simplicity of body musculature, tongue and hemipenial texture, and by peculiar, apparently primitive, characters of squamation. The *Rectus superficialis*, a ventral muscle covering the *Pectoralis* in limbed forms, is absent except in a few agamids. Other trunk muscles are reduced or absent (pp. 377–385). Except in the chameleons the tongue is broad, thick and papillate and is not divided into anterior and posterior portions. The hemipenes lack flounces and plicæ and are of simple texture covered with fine calyculi. There is generally little or no correspondence between the segmentation of the body and the ventral scales. The latter are usually small and rarely number less than four (p. 400) over each segment. The scales when imbricate are easily separated from the skin owing to their loose basal attachment (Fig. A).<sup>1</sup> Osteoderms are rarely present and then apparently in a primitive diffuse state (pp. 395–397). A parasternum occurs in some forms and attains a peculiar development in the arboreal *Uroplates* and *Chamæleon* (pp. 386 and 390). The caudal chevrons are always attached intercentrally (p. 376). The intermedium is curiously enough almost universally absent or fused with the ulnare (pp. 376–377). The patella ulnaris is usually bony (p. 408). An enlarged endolymphatic system is frequently exhibited (p. 414).

This complex group includes many most highly specialized arboreal types, a few exceedingly primitive terrestrial “relicts,” and some forms of aquatic and semi-aquatic habit, but no highly modified burrowers or snake-like, grass-dwelling genera. There is no apparent tendency for the reduction of limbs and girdles. The loss of limbs together with the necessary specialization of body musculature required by a snake-like or a burrowing, worm-like habitus, is never accomplished. Many arboreal tendencies not found in other groups are shown. Sucking laminae are sometimes developed on the toes (*Gekkota* and *Iguania*). The tail is occasionally prehensile in *Gekkota* and *Iguania* and usually so in the

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<sup>1</sup>In some of the Ceylonese agamids (*Cophotis* and *Ceratophora*) the dorsal scales are imbricate and strongly anchored but have the appearance of being enlarged tubercles.



Rhaptoglossa. In the Uroplatidæ, the lateral tail-fringe functions in a most peculiar way as a prehensile apparatus.

The known fossils seem to include the oldest form assignable to the Sauria. This is *Paliguana whitei* Broom, from the Triassic of South Africa.

*Paliguana* is apparently a true lacertilian, although Watson (1914), who has examined the specimen, is not sure of this, and Boulenger (1918a), considers it "problematical." *Paliguana* can scarcely be related to any of the families I have included within the Autarchoglossa.

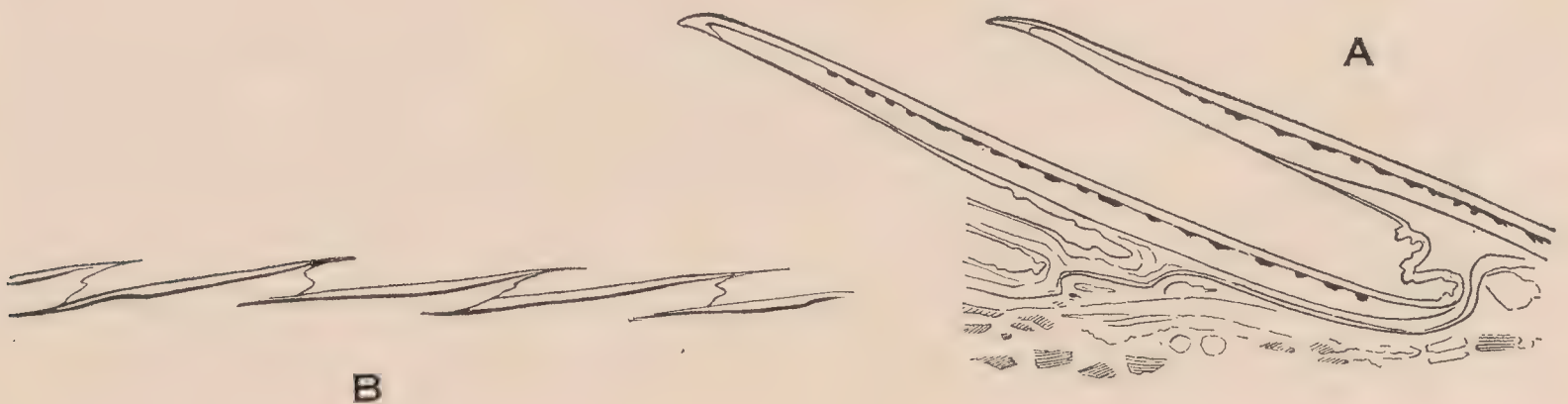


Fig. A. Longitudinal section through the dorsal scales of *Geckolepis polylepis*, adult,  $\times 30$ , after Schmidt (1906-1915, Pl. xxv, fig. 16).

The scales are loosely embedded in the skin in the manner generally found among the Ascalabota.

Fig. B. Longitudinal section through the dorsal scales of *Voeltzkowia mira*,  $\times 22$ , after Schmidt (1910, text-fig. S, p. 626).

The points of Broom's illustrations and description which strike me most forceably are: the large size of the quadrate approached in certain geckos and agamids, and not closely in the Iguanidæ; the small, short squamosal (impression preserved) such as occurs only in the Iguanidæ and Agamidæ; the narrow space between quadrate and jugal, a relation seen only in the Ascalabota, but seldom as exaggerated as here; and the lack of prolonged posterior processes of the parietals, also indicating marked separation from autarchoglossid forms. What is suggested by the little-known teeth would point to gekkonoid affinities, which, of course, the large size of the postorbital arch would negative.

The better-known features would indicate a position among the primitive Ascalabota with resemblances to the Iguania (Iguanidæ+Agamidæ) closer than to the geckos.

### Section Gekkota

This group includes the Gekkonidæ, Uroplatidæ, and the Jurassic Ardeosauridæ. Some of its living members retain the most primitive features of squamation, vertebræ, and branchial apparatus known among lizards.



In most of the genera the vertebræ are amphicoelous and retain the chorda in the intervertebral spaces. A few non-related groups of species are procoelous, having become so secondarily (p. 343). The so-called Eublepharidæ are one of these groups; the sphærodactyloids are another (cf. Noble, 1921).

When procoelous the centra still retain the typical geckonid, short, squarish ventral outline and the condyle is never enlarged (cf. Figs. 3-4). Also, the intercentra remain (pp. 343-344) as fused elements. The tongue is always fleshy and non-extensile and sometimes is decorated with elongate, ribbon-like lappets which develop from the basal villose papillæ. In the recent families no skull arches are ever present; the squamosal is presumably absent; the jugal remains, and there is a strong postfronto-jugal ligament. As in most lizards, there are six cervical vertebræ.

The Mylohyoideus anterior is disposed in a fanwise way, much more markedly so in the Uroplatidæ than in the Gekkonidæ, and develops but a single layer. The Pectoralis, as in many Ascalabota, is extensive, sending a slip to the pelvis in some forms; this may be connected with active arboreal use of the limbs, and the requirements for control of lamellate, sucking digital extremities.

The eyes are usually extremely large with vertical pupils and covered with an immobile transparent eyelid, but in a few genera the eyelids are moveable (*Ælurosaurus*, *Ptenopus*, *Eublepharis*, *Coleonyx*, and *Psilodactylus*).

The interclavicle is rhomboid, cruciform or further reduced; it never becomes a horizontal bar. Osteoderms are rarely present and usually lie diffusely scattered without relation to the superincumbent horny scales (Fig. 83). Dermal cranial ossifications seldom occur, the soft skin usually lying quite free from the skull. Teeth are never present on the palate so far as known. The lacrymal is crowded inside the orbit. The elements of the lower jaw are reduced to five by fusion of the angular and subangular in the Uroplatidæ; in the Gekkonidæ it is the angular and prearticular which join. No pineal foramen; proximal belly of Biceps brachii simple (reduced to a single tendon in *Uroplates*); quadrate relatively large, simple; skull elevated; enlarged endolymphatic sacs frequently present.

Among the exclusively arboreal forms of this group the body often becomes depressed; compression never occurs. A lateral fringe is sometimes developed among the most highly depressed types, and this may extend to the limbs and tail (cf. *Ptychozoon* and *Uroplates*), and to the



feet as a webbing (cf. *Rhacodactylus* and *Ptychozoon*). The claws tend to be reduced in some of the excessively lamellate geckos, and in a simple-toed form (*Chondrodactylus*) are entirely lost.

#### Family †*Ardeosauridæ*

No fossil geckos are known from the Tertiary but von Meyer (1860) has excellently described and figured an important form, *Ardeosaurus brevipes*, from the Lithographic stone of Eichstätt. The age is Tithon, a formation which has been lately assigned to the Jurassic, but some question this and would place it in the Cretaceous.

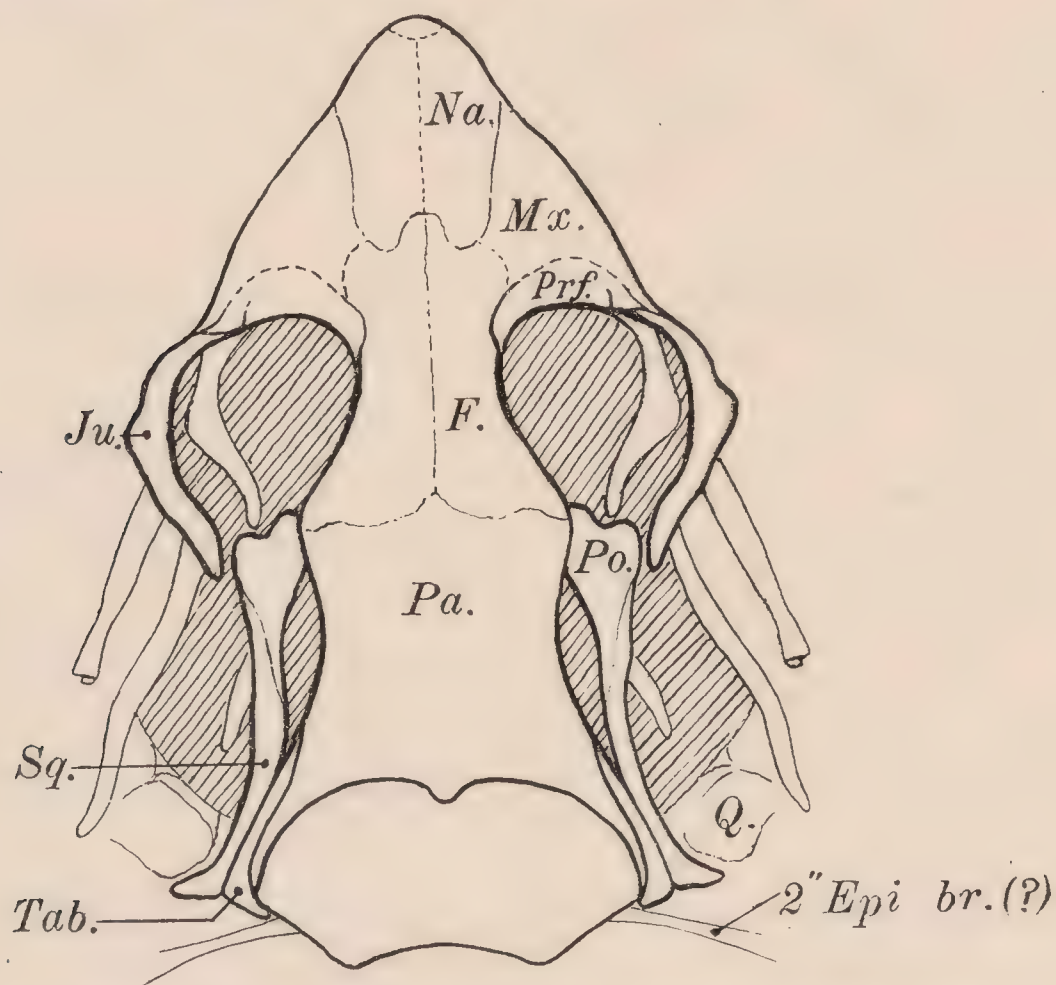


Fig. C. Skull of *Ardeosaurus brevipes*, dorsal view,  
× 4, after von Meyer (1860, Pl. XIII, Fig. 5).

The sutures on the rostrum are doubtful.

Leydekker (1888) has assigned *Ardeosaurus* to the Rhynchocephalia. Nopcsa (1908) calls the genus a "scincoid," without stating reasons. The small reptile is unquestionably a lacertilian as von Meyer supposed it to be. The position of the tabulare and squamosal, the shape of these elements and their relations to the streptostylic quadrate prove this (Fig. C). The broad parietals, narrow supratemporal fenestræ, large depressed vertebræ, paired frontals and elongate squamosal will not allow an inclusion with the Iguania or the Teiidae. The large size of the vertebræ, lack of dermal skull plates, osteoderms, enlarged postfrontals, and the incomplete postorbital arch separate *Ardeosaurus* most decidedly from the Xantusioidea, Scincoidea, Lacertidae and Gerrhosauridae and the Anguimorpha.



The only existing lizards which show the following combination of characters, to be seen in *Ardeosaurus*, are the geckos:—

Vertebræ broad, depressed and at least one-fifth of the body width; parietals broad and flat; nasals and frontals paired, parietals united; postfrontals small; postorbitals small or absent; jugal small, nearly straight and not joined to the postfrontal; hyoid arch (or possibly the second epibranchial) joined to the paroccipital process; six cervical vertebræ; (two cervical ribs preserved); tabulare exposed dorsally; humerus apparently without foramina; no osteoderms or secondary cranial ossifications.

The differences which establish the Ardeosauridæ as a separate family of the Gekkota, perhaps ancestral to the geckos, include:—

Presence of a supratemporal arch and fenestra; an elongate squamosal; a pineal foramen; orbits small, and but little wider than distance across frontals; rostrum pointed. The tail was autotomous by transverse fission of the vertebral centra as in many lizards and geckos, and the fission as indicated by skin impressions in the fossil has left a basal stump shaped much like that of certain geckos. There are no evidences of scales although the outline of the body is preserved. The limbs were short and stout; the neck thick; the body short and much broader than the base of the tail.

The ventral surfaces of the vertebræ and the shape of the vertebral condyles, if present, are not seen on the specimen.

### Section **Iguania**

Vertebræ always procœlous with short tapering centra (moderately elongate in some Agamidæ) and large condyles; tongue as in the Gekkota but never with long, basal filaments, more extensile in the Agamidæ; six cervical vertebræ; the skull arches always present; of normal form or slightly produced posteriorly and upward (*Chamæleolis*, *Phrynosoma*); Mylohyoideus anterior usually in two layers, well separated or, in some Iguanidæ, consisting merely of differently directed fibers,—*Holbrookia*, *Callisaurus*, and *Uma* constitute the only known exceptions (p. 370); Pectoralis sometimes with an abdominal portion strongly developed; eyes small or moderate, normal, never with connivent or transparent, immobile lids, pupil circular; interclavicle usually T-shaped or still further reduced, cruciform in certain Agamidæ (p. 369); osteoderms never developed on the body but a dermal cranial ossification takes place in some iguanids (cf. *Amblyrhynchus*) and obscures the supratemporal fenestra in the highly advanced species, *Phrynosoma* (*Anota*)



*m'callii* (cf. Bryant, 1911); the postfrontal is frequently absent in this group and possibly also in the chameleons (p. 361); the lacrymal is present in the usual position in the Iguanidæ and is frequently absent in Agamids (p. 362); a few pterygoid teeth occur in many Iguanidæ, they are absent in the Agamidæ (p. 365); the clavicles are always present though reduced in the Agamidæ, and are usually simple, though in some iguanids they have retained a perforation (p. 369); the lower jaw is normal, but the splenial is small in Agamidæ (cf. *Rhaptoglossa*) (p. 375); the pineal foramen is rarely absent and undergoes a forward migration in certain species (p. 394) (cf. *Rhaptoglossa*); the proximal belly of the *Biceps brachii* is complex, being usually composed of a fleshy belly and two or more tendinous parts (cf. pp. 403–404); the skull is often elevated, doubtless being secondarily so in connection with the compression of the body; the quadrate is relatively shorter than in the Gekkota; a proscapular process is usually present in the Iguanidæ (p. 411) and is absent in all known agamids with the exception of *Lophura*; enlarged endolymphatic sacs are present in *Anolis sagræ* (p. 414).

In the arboreal members of this group, compression of the body always seems to occur. This tendency reaches its highest expression in the *Rhaptoglossa*. Coincidentally with compression, a strong fold, ridge or series of dermal rays frequently develops along the mid-dorsal line and the claws become specially compressed sharp-pointed, and decurved; those of terrestrial forms are depressed, and have stumpy points, while the horny axis is weaker and the gristly "sole" is heavier than in the arboreals (cf. W. J. Schmidt, 1916, p. 392). In a general way this is true throughout the lizards but the claws of chameleons are peculiarly modified owing to the scansorial form of the feet; and the arboreal autarchoglossids never acquire such perfect climbing tools as do the non-lamellate (and, to be sure, most of the lamellate) ascalabotids.

In the arboreal Iguania the ceratobranchials of the third arch are joined and produced, sometimes extending ventrally to beyond the middle of the sternum. This is part of a mechanism used to dilatate the throat fan frequently present in tree-living forms of this group but unknown elsewhere. The habit of "displaying the gorget," which is often brilliantly colored, is associated with a rapid, emotional play of colors in the skin occurring in certain arboreal forms and in these alone. This is carried to highest attainment in the peculiarly arboreal *Rhaptoglossa*.

The genus *Chalarodon* of Madagascar is certainly an iguanid. The combination of characters of dentition, pattern of throat musculature, and presence of a proscapular process demonstrates this.



Fossil evidence is not absolutely lacking to show the antiquity of the Iguania. *Paliguana* and *Chamops* appear close to what we should expect of stem forms. Tertiary genera from the Eocene of Europe (Quercy) and of North America (Bridger) are possibly referable. *Proiguana* Filhol (1877, cf. de Stephano, 1903) and *Agama galliæ* Filhol seem the most certain. *Iguanavus* Marsh (1872), "*Chamæleo*" *pristinus* and *Palæo-chamæleo europeus* de Stephano are problematical.

### †*Chamops*

There is a specimen referred to *Chamops* and consisting of a portion of a right dentary with several teeth, in the American Museum (No. 988, Dept. Paleont., Laramie Cretaceous, Ceratops Beds, Converse County, Wyoming). The teeth in this fragment agree well with Marsh's description and figures (1892) of *Chamops segnisi* based on an upper maxillary tooth row. Boulenger (1892, 1918a) and Williston (manuscript) have included the latter in the Teiidae. Hay (1901) considers it an iguanid.



Figs. D and E. Portions of right dentary with teeth of *Chamops*,  $\times 4$ , Dept. Vert. Pal., A. M. N. H. No. 988, Laramie Cretaceous.

Fig. D. Outer (buccal) view. Fig. E. Inner (lingual) view.

The teeth are thecodont and set in alveoli (*Alv.*), but are more exposed on the inner than the outer aspect of the jaw. This condition may precede both the highly pleurodont and the hyper-acrodont series of modern lizards.

Marsh's specimen differs from the teiids in having a strictly homodont type of dentition and our specimen seems to agree in this particular. Also the trilobate teeth are not developed anteriorly in the teiids and even in the posterior teeth the lateral cusps are not so large as in *Chamops*. The teeth (Figs. D, E) seem to be closest among living lizards to those of certain non-specialized Iguanidae (cf. *Crotaphytus collaris*), agreeing with these in the swollen base, ratio of height to diameter of crown, form of cusps, in homodonty, and in the fact that a line drawn through the summit of the crowns is straight. They differ in being pleuro-thecodont rather than strictly pleurodont, and they are more completely exposed externally than in recent iguanids.

We may not consider *Chamops* an iguanid on account of lack of definite characters but feel that among living lizards it is most closely



related to that stock. In tooth insertion it seems to partially bridge the wide gap between pleurodont and hyper-acrodon Ascalabota (Iguanidæ and Agamidæ and Rhiptoglossa).

The trilobate teeth of generalized iguanids and agamids and the Rhiptoglossa do not differ materially in form. In the two latter groups such a high degree of acrodonity is attained, coupled with a slicing, shear-like motion of the mandible, that the tooth shafts have come into view more on the outside than the inside of the dentary. To account for this extraordinary digression by closely related groups is a difficulty perhaps best hypothecated by regarding the thecodont or pleuro-thecodont type of tooth insertion seen in Jurassic Euposauridæ and the Cretaceous *Chamops* as a slight advance upon the typically thecodont condition of the Permian *Aræoscelis*. It is obvious that the stage illustrated by *Chamops* would more easily lead, on the one hand, to typical pleurodonity and, on the other, to acrodonity, than the derivation of the highly developed agamid type of acrodonity from iguanid pleurodonity or vice versa (cf. p. 363).

#### †“*Chamæleo pristinus*”

A portion of a right dentary with several teeth of a highly acrodon agamoid type from the Bridger Eocene was redescribed and figured by Leidy (1873) as a rhiptoglossid under the name *Chamæleo pristinus*. This form was also considered by Hay (1901) to be a chameleon. There seems nothing, however, to prevent it from representing equally well a true agamid of the *Calotes* type. After comparison of Leidy's figures with *Calotes* and with *Chamæleon gracilis* and *Chamæleon vulgaris*, I can distinguish no diagnostic peculiarities in the parts preserved in the fossil, between teeth of any of these forms, and therefore prefer to place “*Chamæleo pristinus*” among the Ascalabota as either an agamid or chamæleontid.

#### Section **Rhiptoglossa**

Vertebræ procœlous with elongate cylindrical centra and large condyles; tongue vermiform, highly extensile; only three cervical vertebræ; two skull arches always present and produced posteriorly and upward; pterygoid not in contact with quadrate; no retroarticular process on the lower jaw; Mylohyoideus anterior in two layers corresponding exactly with those in the Agamidæ.



Family **Chamæleontidæ**

Feet zygodactylous, grasping; clavicles reduced or absent; interclavicle absent; nasal bones not bounding nasal apertures; epipterygoid absent.

Pectoralis never with an abdominal portion; body muscles reduced; sterno-hyoid muscles enlarged; eyes large, covered with lids which are connivent except for a pin-hole-like opening becoming a horizontal slit when the animal is at rest; no osteoderms but with dermal cranial and pelvic ossifications in *Brookesia*; postfrontal absent; lacrymal present in the usual position; no pterygoid teeth; splenial absent; pineal foramen very small and located between the frontals; vomers generally fused; os tabulare present; a complete parasternum; proximal belly of Biceps brachii reduced to a single tendon as in *Uroplates*; no os hypischium.

Cope is the only herpetologist who has ventured to regard the Rhip-toglossa as related to the Agamidæ. From additional evidence now obtainable I think Cope's view can be supported. The chameleons, remarkably specialized as they are, show no primitive characters (with the very doubtful exception of the development of a "pro-atlas," cf. Baur, 1886c, and the presence of a rib on the third cervical vertebra) that are not common to the Iguania. There are but few even of the most extraordinary specializations of chameleons which are not at least approached by certain of the arboreal Ascalabota: Geckos (*Phyllurus*) sometimes show an incipient zygodactyly; *Uroplates* wholly resembles the Rhip-toglossa in the loss of body musculature and development of hoop-like parasterna; certain arboreal iguanids (*Anolis*, *Polychrus*, *Chamæleolis*) parallel them in independent mobility of the eyes, diverticulate lung structure,<sup>1</sup> anterior position of the pineal foramen, and casque-shaped head; their great power of color change is equalled if not exceeded by the agamid, *Calotes*. Agamids, generally, share with them the highly important characters, detailed elsewhere, of dentition, hemipenes, composition of lower jaw, and pattern of throat musculature. Agamids also frequently have the prevomers fused and tend to elongate and narrow the vertebral centra (Figs. 5 and 7), and to reduce the clavicle, the interclavicle, the epipterygoid, the tabulare, and the splenial. In the higher agamids the Cervicomandibularis is absent as in the Rhip-toglossa. No lizards except the Iguania and Rhip-toglossa develop highly compressed arboreal forms.

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<sup>1</sup>Beddard (1907) and Methuen and Hewitt (1915) have shown that in some chameleons the lung diverticuli are weakly or not at all developed. Milani (1894) illustrates the strongly diverticulate lung of the iguanid *Polychrus*.



The characters outlined by Boulenger (1887, p. 437) are the most important which have been employed to separate the *Rhaptoglossa* from other lizards. Of these, the first three are shiftings of lacertilian skull elements probably accompanying extreme compression of the body and casque-like development of the head. The fourth (presence of a supratemporal bone [tabulare] as a nodule) rather proves, than otherwise, close association with the true lacertilians, and would not hinder connection with the Agamidæ. The fifth has been spoken of; it is doubtless also connected with bodily compression as the conditions in agamids would indicate. The sixth and seventh (structure of feet and tongue) are highly adaptive features not known in similar degree elsewhere. Connected with the peculiar functioning of the tongue and development of an enormous sternohyal musculature arising in the mid-sternal region, the neck has been shortened and stiffened, either by the dropping out of three vertebræ, or else by the shifting forward of the shoulder girdle a corresponding number of segments.

There would seem few or no objections from morphological or distributional viewpoints against deriving the chameleons from highly developed agamids at the beginning of the Tertiary.

The fossil record shows no undoubted chameleons; all those so described are jaw fragments and can equally well be placed with the Agamidæ.

#### Division **AUTARCHOGLOSSA**

*Rectus superficialis* always present; hemipenes usually flounced or plicate; less than four, and usually only two, rows of ventral scales to each body segment; scales, when imbricate, with narrow free margin and firmly attached to the skin (cf. Fig. B); osteoderms frequently present and never entirely diffuse (Figs. 84–98). A parasternum often occurs and attains considerable extent only in the burrowing forms (p. 387); caudal chevrons attached intercentrally or centrally; intermedium sometimes present; epipterygoids occasionally absent; patella ulnaris rarely bony. The tongue is variously developed but is like the *Ascalabota*, only in the *Zonuridæ*.

None of the high arboreal specializations of the *Ascalabota* ever appear in this terrestrially inclined group. There are no digital or caudal lamellæ, no prehensile tails, no excessive flattening or compression of the body. On the other hand remarkable subterranean and snake-like modifications are frequently acquired.



The body musculature is more complex even in the limbed forms than in the Ascalabota (pp. 377–385) and the belly musculature, specially developed, seems usually to help along the action of the limbs in walking. This allows the limbs to gradually disappear, on occasion, without hindrance to locomotion. The limbs may act as an encumbrance in the case of burrowing or grass-dwelling forms. They appear to dwindle only in correlation with such habitats.

The most advanced burrowing types sometimes lose the pectoral girdle completely, develop a complete dermal covering over the eye and ear, lose the skull arches, the interorbital septum, the epipterygoid, the median skull sutures, and gain body musculature of greatly increased complexity,—sometimes with specially developed skin layers and sets of bundles running from ribs to skin so arranged as to allow both backward or forward motion, underground and on the surface. The tail always becomes very short in the burrowers and the caudal chevrons shorten and in an extreme case (*Dibamus*) are entirely absent. The extra-columella, in absence of a tympanum, may greatly enlarge as in the Amphisbænidae to function from the side of the jaws and face (cf. Figs. F, G). Such an arrangement may serve as a microphonic device to detect noisy insectivorous prey such as termites.

In the limbless grass-inhabiting forms, the profound developments seen in the burrowers do not occur. The skull arches are never lost (except in Pygopodidae, p. 345); the skull elements reduced in the burrowers remain as normal; the girdles remain; the body musculature gains in extent in various ways but not as in the burrowers. There is never a large Cervicomandibularis muscle developed to swing the head, as in burrowers. Only the normal Scapulae (skin slips) are developed and never extra sets. The tail always becomes very long and brittle and the caudal chevrons sometimes fuse with the centra. The eye remains normal and the ear does not close (*Ophiodes striatus* has a closed ear and may be an exception).

The snakes appear to have arisen from anguimorphid, grass-living lizards. The burrowing snakes (Typhlopidae and allied families) parallel the burrowing lizards in many profound ways and would seem to be derived from autarchoglossid stock for that reason and because of the paleotelic characters they hold in common with the Anguimorpha (p. 301).

#### Section **Scincomorpha**

Tongue scaly or with oblique plicæ (pp. 374–375); hemipenes laminate; clavicles when present usually dilatated, often perforate and sometimes hook-shaped (Figs. 78–80); osteoderms when present com-



pound (except dorsally in Gerrhosauridæ) and ventrally not corresponding in extent with the horny scales (pp. 395–397); tooth replacement often directly successive by intrusion of new tooth into hollow base of old (p. 364); caudal chevrons, when present, always intercentral or slightly post-intercentral (p. 376); teeth usually hollow, cylindrical, obtusely pointed or rarely (Teiidæ) broader and with small lateral cusps.

The tongue, osteodermal, tooth, and clavicular structures separate this group more widely from the Anguimorpha than external appearances might indicate. Another point of distinction is to be found in the simplicity of the throat musculature as detailed under the various superfamilies. The primary throat musculature is obscured in the burrowing members of this group, and not elsewhere (cf. *Anniella*, and *Typhlops*), by supergrowth of the terminal fascia of the Cervicomandibularis which is actively used in turning the head while burrowing. In *Feylinia* and *Dibamus* the terminal fascia entirely covers the throat and the muscle extends a great way down the body. In the amphisbænians certain processes of the lower jaw (cf. Peters, 1882) are provided for the attachment of this muscle.

Degenerative tendencies in the group appear to be first to lose the hind limbs (except in *Neoseps* and in the Dibamidæ where the hind limbs, present only in the male, appear to be used as claspers) and then the fore limbs (p. 354), but, while the pectoral girdle may in extreme cases entirely fail, rudiments of the pelvis always remain. In the girdle itself the clavicular parts are the first to disappear. Degenerate forms are found in all families except the Lacertidæ and Xantusiidæ.

#### Superfamily **XANTUSIOIDEA**

Vertebræ procœlous with extremely small geckonoid condyles, squarish centra, and tiny, persistent intercentra fused with the condylar balls (Fig. 8); hemipenes peculiar (cf. Cope, 1900, p. 541); Rectus lateralis closely attached to the ventral scales as in lacertoids; Mylohyoideus with a few large interdigitating bundles; ventral scales usually squarish, non-imbricate as in lacertoids and some other autarchoglossids; dorsal scales granular; femoral pores present; no parasternum.

#### Family **Xantusiidæ**

Vertebræ almost exactly as in the procœlous gecko *Coleonyx* (cf. Figs. 4 and 8); supratemporal fenestra closed by union of squamosal and parietal bones; clavicles dilatated and perforated; interclavicle cruciform; Mylohyoideus without superficial anterior bundle; a few fibers of Genioglossus run to the skin partly on the body simulating the Genio-



myoideus muscle of the Anguioidea; no osteoderms; dermal skull-roof present; parietals distinct.

The presence of an archaic type of vertebræ would indicate a position among the Gekkota were it not for the assemblage of purely autarchoglossid characters in the musculature, ventral squamation, and tongue. The group is an isolated one and should be placed as the most primitive of the Autarchoglossa on the basis of the geckonoid characters, and by reason of the nearly complete third branchial arch (p. 339) and the free intermedium (p. 377). Were it not for the intermediate position and relationships of this family, one could derive the Scincomorpha and Anguimorpha from iguanoid stock, as Cope has done.

#### Superfamily **SCINCOIDEA**

Vertebræ procoelous with large condyles, tapering centra and no intercentra (Figs. 10, 11); Rectus lateralis not closely fused with the ventral scales; Mylohyoideus simple and usually with many regularly interdigitating bundles; scales cycloid or rhombo-cycloid, strongly imbricate; no femoral pores; rudiments, at least, of a parasternum.

Filhol (1882) refers his *Cadurcosaurus sauvagei* to the scincs. The form was described on a lower jaw with an enlarged posterior crushing tooth. *Dracænosaurus croizeti* Gervais (1859) is a similar genus from the Oligocene and has been placed with the scincoids by Lydekker (1888). The identification of jaw fragments such as these is questionable.

A scincoid lizard, *Didosaurus mauritanicus* Günther, has been described from a marsh deposit on the island of Mauritius. The locality is referred by Nopcsa (1908) to the Pliocene, but the fauna is certainly not older than Pleistocene and contains remains of recently exterminated animals.

*Didosaurus* has resemblances to the scincs in the structure of the mandible, the short teeth, the closure of the Meckelian sulcus beneath the internal border of the coronoid, the pattern of the scale-plates on the fused frontals, and the shape of the vertebræ. Resemblances to *Cyclodus* which Gadow mentions, do not seem close on account of the number of teeth, twice as great as in *Cyclodus*.

#### Superfamily **LACERTOIDEA**

Vertebræ as in Scincoidea; Rectus lateralis closely fused with the ventral scales; Mylohyoideus as in Scincoidea; ventral scales usually squarish, sometimes non-imbricate; dorsal scales granular or imbricate; femoral pores present; a parasternum in some of the Teiidae.



The characters of the *Gerrhosauridæ* are intermediate between those of the typically *teioid* members of this family and the *Scincidæ*.

The ventral scales of *Gerrhosaurus* are imbricate and cover osteoderms of compound nature similar to those of the *scincoids* (Figs. 88, 89). In the *Lacertidæ* osteoderms are absent on the body and remain as a dermal covering over the skull. In the *Teiidæ* there are no traces of osteoderms even on the skull.

A number of fossil lizards have been referred to the genus *Lacerta*. Of these the best established is *Nucras*, an existing African lacertid which has been found enclosed in Oligocene amber from East Prussia (cf. Klebs, 1910, and Boulenger, 1891*a*, 1920). On Boulenger's authority, the Upper Eocene *Lacerta mucronata* Filhol (1877; cf. de Stephano, 1903), is close to the living species *agilis*.

Lartet (1851), Pomel (1853), and others have described fossil species of *Lacerta* from Miocene, Pliocene, and Pleistocene formations of Europe. Many of the determinations seem based on too scanty material (cf. Nopcsa, 1908).

Ambrosetti (1887), and Rovereto (1914) have examined remains of large *teiids*, close to the living genus *Tupinambis*, from Oligocene and Pliocene localities in Argentina. The systematic determinations are quite convincing.

### Superfamily **AMPHISBÆNOIDEA**

Vertebræ with broad, flat centra and wide condyles (Fig. 9), sub-central arterial foramina present as in *geckonids* and *pygopodids*; no neural spines, no intercentra; *Rectus lateralis* attached closely to the belly scales and greatly extended, reaching the dorsal mid-line in some forms; dorsal scales granular or tubercular when present; skin usually naked; no parasternum; preanal pores present.

### Family **Amphisbænidæ**

No osteoderms; no skull arches; no interorbital septum; no epipterygoids; pre-maxillaries single; extra-columella enormous (Figs. F, G).

The rudimentary pelvis resembles that of degenerate *scincomorphs* and is not like that of limbless *anguimorphs*. The tongue and hemipenes also show *scincomorph* affinities. The skull and cervical vertebræ are remarkably specialized and the complexity of the body musculature is greater than that of other *Squamata* except the burrowing snakes, *Typhlops*, which greatly resemble the *amphisbænians* in this adaptational particular. The *Cervicomandibularis* is enormous, as in other burrowing



scincomorphs but not as in the degenerate subterranean anguimorphs and the burrowing snakes, where it is small or moderate. The tail is exceptionally short even for a burrowing lizard but caudal chevrons (lost in the Dibamidæ) are still present. A spade-like development of the tail is sometimes seen with enlarged frictional tubercles in *Rhineura*, as in the uropeltid serpents. External limbs are present only in the single genus *Bipes*. The pectoral girdle is entirely wanting in some forms. The teeth vary in the subfamilies from pleurodont to acrodont and the number of annuli over each body segment becomes reduced to one in some of the Old World forms and apparently becomes doubled again in *Trogonophis* (pp. 399–400).

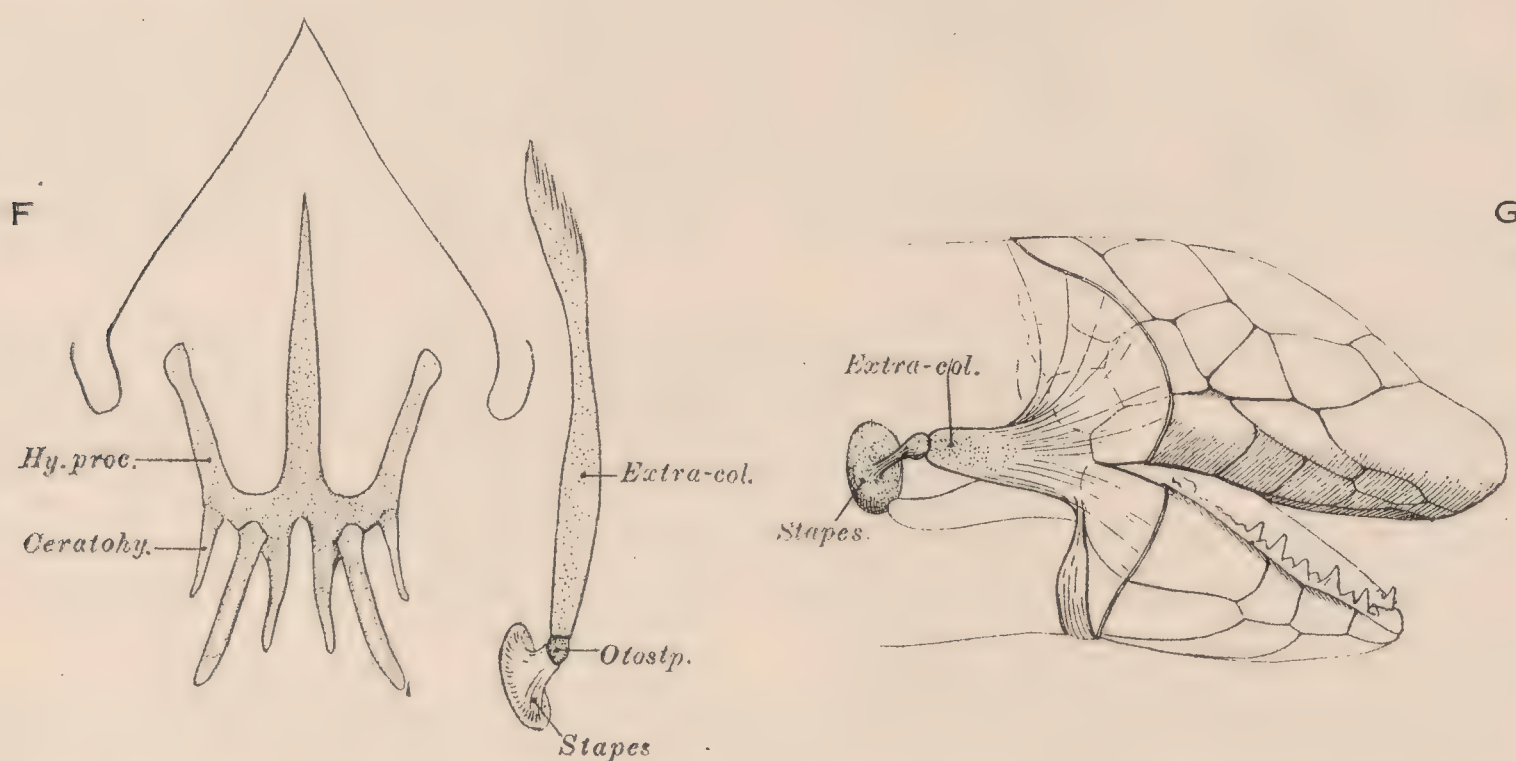


Fig. F. Hyoid apparatus and enlarged extra-columella of embryo of *Amphisbæna cæca*,  $\times 15$ , A. M. N. H. No. 13146.

A small ceratohyal (*Ceratohy.*) remains and its location proves that an extended basihyal process (*Hy. proc.*) is present as in teiids. No direct continuity between the tip of the extra-columella and the hyoid is thought possible.

Fig. G. Extra-columella *in situ* of the amphisbænid *Rhineura floridana*,  $\times 4$ , A. M. N. H. No. 5724.

Functional significance of the enlarged extra-columella is indicated by its attachments to the fascia extending into the spongy tissue surrounding the jaw.

The resemblances to the degenerate Teiidae are for the most part secondary but are nevertheless indicative of ancestral relationship to that family, as is also the fact that the anterior process of the basi-hyal is exceptionally long, as it is in all known teiids (cf. Fig. F).

The locomotory and burrowing habits are exceptional, the double sets of Scapulae (which are so developed also in *Typhlops*) permitting movements forward or backward with equal facility (Fig. 40).

The great morphological variation and scattered distribution of this group as well as its isolated position as one of the most highly modified



lacertilians lead one to expect the antiquity which is indicated by the fossil record.

Close relatives of *Rhineura* are found in the Oligocene of North America (White River) along with numerous other genera, represented by vertebræ and skulls, one of which (*Hyporhina* Baur) shows a persistent postorbital arch (cf. Baur, 1893 and Douglass, 1908).

### Section **Anguimorpha**

Tongue smooth or papillate; hemipenes flounced and often pocketed or repand (p. 358); clavicles always present and simple; osteoderms, when present, never compound and usually corresponding in extent with the horny scales; teeth frequently conical, pointed, recurved, and, except in Zonuridæ, without lateral cusps, with alternate replacement and with shafts more solid than in the Scincomorpha; caudal chevrons often attached to the middle of the centra; no parasternum except in *Chamæsaurosa*.

The throat musculature is complex (cf. Figs. 54-61), except in the Zonuridæ, where it has iguanoid resemblances. In the burrowing members (and in the serpents) the Cervicomandibularis does not enlarge. This has doubtless to do with the fact that the construction of the lower rami (loosely articulated anteriorly) does not favor such a method of moving the head while burrowing.

In degradational forms the fore limbs are first lost and the clavicles seem to maintain a slower rate of reduction (pp. 352 and 354) than the scapulo-coracoid and sternum.

Degenerate forms are not found among the Platynota, Helodermatidæ, and Xenosauridæ.

Fossil remains perhaps referable to this group have been discovered in the Upper Jurassic and were described by Lortet (1892) as the Euposauridæ.

### Family †**Euposauridæ**

A nearly complete and finely preserved skeleton of *Euposaurus thiollieri* Lortet (1892, Pl. VI), shows saurian characters quite satisfactorily in the absence of a lower quadrato-jugal bar, the lacertilian pes (cf. Boulenger, 1893), the six cervical vertebræ, double sacral articulation, and the single-headed ribs.

On the basis of pleurodont dentition, absence of supratemporal fossæ, and non-dilatation of the clavicles, Boulenger considers that the characters approximate those of the Anguidæ.



The teeth do not appear to be strictly pleurodont and are possibly not at all so. Some, in Lortet's figure, are set in sockets, while a few appear to have broken through the lingual walls of the alveoli to lie as pleurodont teeth do. The teeth are small, pointed, and slightly recurved at the extreme tip. The skull roof appears to be covered with secondary encrustation, a feature which should place this family among the Autarchoglossa as might also the combination of extremely short propodials with very long metapodials in the hind limb, and the elongate, narrow, lacertid-like body. The clavicles appear to be simple, but are not certainly so. This would allow a reference with the Anguimorpha about as Boulenger has suggested.

If the other species referred by Lortet to *Euposaurus* can be so considered, as may appear doubtful, the family had attained considerable radiation in respect to length of body, limbs, and feet, and size of head, a differentiation not to be unexpected among any group of Ascalabota but scarcely found in this form among the Autarchoglossa. It might be recalled that a secondary dermal skull-roof does occasionally occur among living iguanids. Williston (manuscript) placed the Euposauridæ in his serial order between the Gekkonidæ and Agamidæ. I should allow this family a provisional situation in the Anguimorpha.

The family characters seen on Lortet's specimens include:

Teeth thecodont or subpleurodont; cranial ossifications present roofing over the supratemporal fenestræ; frontals fused; orbits large, directed dorsally and with a posterior emargination; quadrate bones narrow; clavicles simple (?); no parasternum (?); vertebræ broad, depressed (?).

#### Subsection **Platynota**

Seven or more cervical vertebræ; dorsal vertebræ of highly modified procœlous type (Figs. 22–26); centra short, cylindrical, or tapering; condyles very large and with flanges well-developed; caudal chevrons pediculate and articulated (rarely fused) near the middle of each centrum; no transverse suture in the caudal centra; nasals elongate, fused; premaxillaries elongate; lower jaw with median transverse sutural joint or a well-developed joint (Mosasauroidea); a parietal foramen; no osteoderms or bony skull plates; dorsal scales granular, (rhomboid on some parts in *Varanus* and in the aigialosaurs, dolichosaurs, and mosasaurs, cf. Nopcsa, 1903).



Superfamily **VARANOIDEA**

Centra depressed; condylar surfaces but little apparent in ventral view; clavicles and interclavicles present<sup>1</sup>; a lacertilian sacrum; digits with claws and without hyperphalangy; sclerotic ring cartilaginous.

Family **Varanidæ**

Postorbital arch usually incomplete<sup>2</sup>; frontals divided; seven cervical vertebræ; dentition subpleurodont; limbs normal, ambulatory; propodials elongate.

The existing species form a peculiarly isolated group with the following outstanding characters; tongue smooth, slender, elongate, extensile, deeply forked, and sheathed posteriorly as in the serpents; Mylohyoideus anterior concealed beneath the extensive Mylohyoideus posterior and the fascia of the Geniohyoideus and Cervicomandibularis which are specially developed in connection with the median mandibular joint; interclavicle anchor-shaped; hyoid arch broken at the basi-cerato-hyal joint, as in some Diploglossa; ventral scales small in comparison with those of other autarchoglossids; epipubis double.

The living species, despite considerable radiation in habitat, are very conservatively modified, being now placed within the one genus *Varanus*. The food habits are carnivorous or moluscivorous. Aquatic, subaquatic, terrestrial, and thoroughly arboreal forms are included. The extinct members form a long line of descent since the Lower Eocene. The early forms seem extremely like the living genus, and the Old World members, forty-one species in all, occurring in Eocene, Oligocene, Miocene, and Pliocene formations, are referred by Fejérváry (1918) without exception to the living genus, *Varanus*.

The North American Eocene genera differ from the known Old World stock in characters that may be recapitulated here.

†**Saniwinæ**, new subfamily

To include *Saniwa* Leidy (1870) and *Thinosaurus* Marsh (1872) from the Lower and Middle Eocene of North America (Huerfano, Wasatch, and Bridger formations).

Dorsal vertebræ resembling recent *Varanus* but not so short and with a less-marked precondylar constriction (cf. Figs. 24, 25); condyles not relatively as broad as in Varaninæ; a zygosphenal articulation is present in *Thinosaurus*, less marked in some species, and absent in *Saniwa*.<sup>3</sup>

<sup>1</sup>Perhaps lacking in Dolichosauridæ.

<sup>2</sup>Some recent Varanidæ are known to develop a complete jugal arch as a variant (Fejérváry, 1918).

<sup>3</sup>Gilmore in a recent paper (1922, Proc. U. S. Nat. Mus.) states that the type specimen of *Saniwa* has small zygosphenes and zyganttra. Forms related to *Saniwa* and represented in the American Museum collections appear to have no zygosphenal articulations. Gilmore finds that the type skull of *Saniwa* is very like *Varanus*.



A single tooth, referred by Leidy to *Saniwa ensidens*, is varanoid; being conical, recurved, sharp-pointed, smooth and thick-walled, but differs from typical *Varanus* in its "rhomboidally oval" base.

The caudal chevrons are articulated as in the Platynota generally.

The other known Varanidæ may be divided as follows:

†**Varaninæ**, new subfamily

To include *Varanus*, and possibly all the Old World Tertiary forms (excepting the Megalaninæ).

Mid-dorsal vertebræ short, with pronounced precondylar constriction; condylar surfaces scarcely apparent in direct ventral view; condyles relatively larger than in the Saniwinæ; no zygosphenes and zygantrum.

†**Megalaninæ**, new subfamily

To include the Megalanidæ of Fejérváry (1918),—Pleistocene ?, Australia.

Mid-dorsal vertebræ very short, broad; an extremely pronounced precondylar constriction; condylar surfaces not greatly apparent in direct ventral view, condyles broader than in Varaninæ; a zygosphenes and zygantrum (Fig. 26).

The vertebræ of the Saniwinæ, as well as what is known of the teeth, point to characters in this group more like those of less specialized anguimorphs. The gigantic megalanians may be considered as the most highly developed terrestrial branch of the Platynota.

Family †**Aigialosauridæ**

This family, known only from the Lower Cretaceous (Neocomion) of Europe, includes the following genera (Nopcsa, 1903): *Aigialosaurus* Kramberger, *Carsosaurus* Kornhuber, *Opetiosaurus* Kornhuber, ? *Mesoleptos* Cornalia.

The skeleton and squamation resembles that of *Varanus* in some detail but there is a complete postorbital arch, the frontals are fused, the dentition as in the mosasaurs is subthecodont, large pterygoid teeth are present, and the limbs are shortened and the feet broadened, doubtlessly in connection with subaquatic habits.

Boulenger (1891a, 1893) regarded this group, with the dolichosaurs, as ancestral to all other lizards, mosasaurs, and serpents. Kramberger (1892) held similar views. Dollo (1892, 1904) considers the aigialosaurs as derived from true lizards near the Varanidæ and as ancestral to both Dolichosauridæ and Mosasauridæ. Nopcsa (1903) reaches the same



conclusions, apparently independently. Williston (1904) also adopts this opinion, emphasizing the varanoid affinities of the aigialosaurs and dolichosaurs. I hold this view, and regard the presence of the annectant Aigialosauridæ as grounds for denying rank higher than that of a superfamily to the mosasaurs.

#### Family †**Dolichosauridæ**

This family is distinguished from the Varanidæ and Aigialosauridæ by the presence of thirteen cervical vertebræ and in the relatively small, short skull, small, short limbs, elongate, serpentiform body and tail, possible lack of clavicles and interclavicles, and lack of preacetabular pubis. The dentition, as in *Varanus*, is subpleurodont; the frontals are separate, and a postorbital arch is present.

The group is known only from the Cretaceous of Europe, and includes under the authority of Nopcsa (1903), the genera *Dolichosaurus* Owen, *Acteosaurus* von Meyer, *Pontosaurus* Kramberger, and *Adriosaurus* Seeley.

The so-called "ophidian" characters of the aquatic dolichosaurs (cf. Nopcsa, 1908) are paralleled in many other non-related lizards (cf. p. 345). Of these characters the small skull, zygantral articulations, cylindrical body, and reduction of extremities do not of themselves indicate serpent relationship; nor does the elongate neck, since we cannot tell whether or not the cervical vertebræ of snakes have been increased above those of lizards (cf. Janensch, 1906). The paleotelic characters held in common with the Serpentes are those of platynotine lizards in general. Furthermore, it is difficult to see how a group so highly modified in body form could be ancestral to the mosasaurs.

#### Superfamily †**MOSASAUROIDEA**

Postorbital arch complete; seven cervical vertebræ; centra cylindrical; condylar surfaces directed posteriorly; dentition subthecodont; clavicles and interclavicles greatly reduced or absent; limbs paddle-shaped, without claws and with hyperphalangy; sclerotic ring bony.

Three, perhaps four, adaptive types of mosasaurs are recognized (Williston, manuscript). These include: (1) surface, swimming forms "with elongate trunk composed of as many as thirty-five dorsals, the tail with pronounced subterminal dilatation, zygosphenes, a well ossified carpus and only slight hyperphalangy,"—*Mosasaurus* and *Clidastes*; (2) deep sea forms "with proportionally shorter neck, less elongated trunk with but twenty-one vertebræ, a more uniformly flattened tail, less well-



ossified carpus and tarsus and greater hyperphalangy,"—*Platecarpus*; (3) "a diving type, with more elongated head, heavy cartilaginous protections for the ears, a relatively short neck, body with but twenty-two vertebræ, a longer and much flattened tail, almost entirely cartilaginous mesopodials and highly developed hyperphalangy,"—*Tylosaurus*; and (4) possibly a littoral, molluscivorous genus, *Globidens* Gilmore (1912), in which the teeth were rounded and rugose.

In *Globidens* the replacing teeth are pointed before they become functional. In *Varanus niloticus*, a cancrivorous and molluscivorous monitor with rounded teeth, the teeth in the young are pointed (cf. K. P. Schmidt, 1919).

The osteology of the mosasaurs has been studied extensively. Far more material has been handled than of any group of recent lizards. Yet, curiously enough, disagreement still prevails regarding their descent and place in the system.

The history of this controversy has been reviewed by Baur (1892) Williston (1898), Nopcsa (1903), and Dollo (1904). Those who have favored varanoid relationship of the mosasaurs and have generally regarded them as something less than a division of the Squamata separate from lizards are: Cuvier, Goldfuss, Owen, Marsh, Baur (1892, 1895, 1896), Merriam (1894), Williston (1898, 1904), Nopcsa (1903, 1908), and Versluys (1907).

Those who have considered varanoid relationships as questionable or distant are: Cope (1869, 1878, 1895*a*, 1895*b*, 1896*a*), Boulenger (1891*a*, 1893), Dollo (1892), Kramberger (1892), Osborn (1899), Fürbringer (1900), Gadow (1901), and Fejérváry (1918). Von Huene (1910) is non-committal.

Osborn writes (1899, p. 187): "Besides the secondary degenerate adaptation to marine life shown in the girdles and appendicular skeleton, there are certain fundamental differences in the basioccipitals (p. 170) and ribs (p. 176), in fact in all parts of the skeleton. These differences . . . do not even justify the assertion that the Varanidæ and Mosasaurs sprang from a common stem."

The basioccipital processes are less developed in *Varanus* than in any other lizards I have examined with the exception of the specialized Uroplatidæ. This is a feature apparently correlated with the strength and degree of tendinous insertion of the long subcervical muscles. The process is absent in some varanids, present as a small tubercle in others, and may be further developed as a considerable swelling. From its variability in the Varanidæ I should not be inclined to regard its presence in Mosasaurs as grounds for distinct separation.



A point is made of the *Sphenodon*-like tendencies of the ribs in *Tylosaurus*. This, it is shown, is most apparent in their shape and curvature, in the position of the diapophyses of the dorsal ribs, and in the general form of the chest.

The ribs in both *Varanus* and *Tylosaurus* are flattened. The curvature, as shown by a skeleton of *Varanus* at hand, and by placing the disarticulated ribs directly upon a photograph of the ribs of *Tylosaurus*, lying in place as they were found, is almost exactly the same in the two genera. The expansion of the anterior dorsal ribs is shown almost equally in *Varanus* and in *Tylosaurus*. In the most anterior dorsal rib of *Tylosaurus*, there seems to be no more vertical flattening than in the specimens of *Varanus* at hand. The rib differences cannot be considered a strong objection to varanoid relationships.

The form of the chest depends largely upon the correctness of Dr. McGregor's restoration of the sternum. If the ten anterior dorsal ribs had a sternal connection as shown in the restoration, profound divergence from the usual lacertilian condition would be indicated. No sternal rib connections are actually seen on the specimen but the direction of the anterior five dorsal ribs, at least, would suggest sternal attachment for these. The posterior five cartilaginous ventral rib-ends may well have lain free in ventral intercostal muscles, as in many lizards, and the comparatively small sternum may not really provide attachment for so many ribs. The specimen as it lies shows no marked departure from lacertilian conditions in relative position of sternum and cartilaginous ribs.

The form of the axis and the two rounded anterior intercentra are considered by Osborn to represent primitive features in the skeleton. The number and position of the elements of the axis and the lack of fusion of the axial intercentrum are the same in *Varanus* and the Mosasaurs. Can the rounded form of the intercentrum be considered primitive? If the ring-shaped intercentrum of *Varanus* represents the element occurring in the amphiœlous geckos and many other lizards, as should be unquestionably the case, and if we may consider the gekkonid condition as primitive on the basis of its close resemblance to certain Permian Cotylosaurs (p. 343), (and also owing to the fact that in geckos the intercentra persist and are half-ring-shaped throughout the dorsal region), we may certainly consider the half-ring-shaped centra of other lizards as of primitive shape and should hesitate to regard the mosasaurid condition as anything but a secondary development.

Followers of Baur, Williston, and Nopcsa will perhaps be surprised to find that Fejérváry (1918) is not inclined to regard the Aigialosauridæ



as intermediate between the Varanidæ and the mosasaurs. Williston (1904) holds that "there are no more striking examples of evolution presented in all vertebrate paleontology than that of the aquatic mosasaurs of the Upper Cretaceous, through the semi-aquatic aigialosaurs of the Lower Cretaceous, from the terrestrial varanoids of the lowermost Cretaceous or Upper Jura." Fejérváry retorts: "I must doubt of so striking a transformation taking place in comparatively so short a time," and adopts the Osborn-Fürbringer conception of separate origin of varanids and mosasaurids. All this in the face of the fact that among the thousands of specimens of mosasaurs so far collected not a single one has been taken below the Upper Cretaceous! It is curious that Fejérváry's long, slow evolution of the mosasaurs has left us no trace.

I am inclined to retain the mosasaurs as a superfamily of the Platygota as Baur has done. This is suggested by the shape and position of the skull elements, the teeth, the median mandibular joint, the vertebræ, the shape of the interclavicle when present, the formula of the scapulo-coracoidal fenestræ, the central pediculate articulation of the caudal chevrons, the lack of osteoderms, cranial plates, and parasternum, the lingual furrows in the prevomerine bones, and the shape of the scales.

#### Subsection **Diploglossa**

Six cervical vertebræ; dorsal vertebræ of normal procœlous type (except in Pygopodoidea); centra not constricted in front of condyles; no condylar flange; proximal belly of Biceps brachii often with a posterior tendon and an anterior fleshy portion, the opposite of what usually occurs (p. 404); caudal chevrons central and pediculate only in the Glyptosauridæ, otherwise when central (limbless Anguidæ and the Anniellidæ) ankylosed to the centra as in the Serpentes; osteoderms present in all families except the Pygopodidæ, never compound, and sometimes (Glyptosauridæ, Xenosauridæ and slightly in Helodermatidæ) ornamented with tubercles; dorsal scales imbricate except in the Helodermatidæ and Xenosauridæ.

Most of the footless members of this group are grass-living, practically non-burrowing forms, such as are rarely developed among scincimorphs (cf. *Tetradactylus*).

The girdles are never profoundly reduced except in the Anniellidæ and in a few Pygopodidæ. In these, closed eyes and ears, and shortened tails point to a burrowing habitus. *Anniella* shows close similarities to the Anguidæ, and especially to *Gerrhonotus*, as expressed in the pattern of the mylohyoid, the hemipenes, and in other characters determined by Baur (1894) and Coe and Kunkel (1906).



The Pygopodidæ and Helodermatidæ include the only non-burrowing forms, except the geckos, that lose the supratemporal arch. A hypoischial cartilage is generally present (pp. 405–406). In the degenerate *Pygopus* it divides, half going with each of the well-separated ischii. The same phenomenon occurs in the degenerate anguid, *Ophiodes*; this may occur in the serpents but is unknown in other groups of lizards.

#### Superfamily **ANGUIOIDEA**

Vertebral centra tapering, not constricted medially; condyles not nearly as wide as the centra except in *Ophisaurus* where the condyles are varanoid, but where there is no precondylar constriction as in the Varanoidea; ribs in *Ophisaurus* with a dorsal muscular process but no ventral process; no femoral or preanal pores; a geniomyoid muscle (p. 373) such as occurs in no other lizard with possible exception of *Xantusia*; teeth solid; tooth replacement alternate (pp. 363–364).

This superfamily has many superficial resemblances to the Scincoidea, but scarcely any of the paleotelic characters common to that group, being more specialized in hemipenial texture, pattern of throat musculature, osteodermal structure, fusion of skull elements, variations in position of caudal chevrons, variation in tooth replacement, and other features.

The pattern of the throat musculature indicates close affinity between the families Anguidæ, Anniellidæ, and Xenosauridæ. The Helodermatidæ are included because of the presence of a Geniomyoideus muscle, and because of their relationship to the Glyptosauridæ,—true anguioids which are in some characters intermediate between the Anguidæ and Helodermatidæ.

The greater number of species of the two latter are distributed in southwestern North America. The Anniellidæ and Xenosauridæ are monotypical and confined to that region.

Fossil genera referable to the Anguidæ include forms from the Miocene of Europe. Some of these closely resemble recent *Ophisaurus*. The best known is *Propseudopus fraasii* Hilgendorf (1885) described from a complete skeleton taken at Steinheim. The ribs have a dorsal tuberculum-like process as in *Ophisaurus*, the skull, teeth, and osteoderms are also similar to *Ophisaurus*. The generic distinction rests upon the greater number of teeth on the prevomers.

Hilgendorf includes von Meyer's *Pseudopus*, from the Oligocene of Bonn (later described under the name *Pseudopus moguntius* by Boettger, *Paleontographica*, Band XXIV), with his genus *Propseudopus*.



Some of the species of "*Anguis*" noticed by Lartet (1851) from Sansan are described as having obtuse teeth as in *Ophisaurus*. Gervais (1859) has redescribed two of Lartet's species.

Gerhardt (1903) has studied a lower jaw with teeth from the Lower Miocene of Ulm and refers the genus to *Ophisaurus*.

#### Family †*Glyptosauridæ*

The lizards of this Tertiary group are characterized by their osteoderms of the simple anguroid type, imbricate on the body, and minutely embossed with small enamel-covered tubercles. Scutes of this nature in connection with a skull fragment were first described by Gervais (1859) under the name *Placosaurus rugosus*. This material was found in the Upper Eocene of Sainte Aldegarde. Other European remains described by Gervais (*Varanus margariticeps*), Filhol (1877, *Plestiodon cadurcensis*; 1894, *Necrodasypus galliæ*), de Stephano (1904, *Diploglossus cadurcensis*) and Leenhardt (1906) are all regarded by Boulenger (1919b) as *Placosaurus*. All are from the Eocene.

Boulenger had the opportunity of studying photographs of the skull of *Placosaurus*, which Leenhardt described, and pronounced the fossil a helodermatid. The absence of a squamosal (supratemporal) arch would separate *Placosaurus* from the American forms, *Glyptosaurus* and *Xestops* (cf. Marsh, 1871, 1872). All known parts of the skeleton of *Placosaurus*, the teeth and the osteoderms, are so similar in the American genera, however, that I am inclined to think a squamosal arch may eventually be found in *Placosaurus*. Depéret (1917) suggests resemblances between the European and American genera.

Douglass (1903, 1908) has described and illustrated portions of skulls of *Helodermoides* and *Glyptosaurus*. He says that a supratemporal arcade is present in his skull of *Glyptosaurus* but the figure does not show this important point satisfactorily. The bone called squamosal by Douglass is evidently the median element (tabulare). Cope (1884) states that both arches occur in *Peltosaurus*. His type specimen does not show this but another fragment of *Peltosaurus* figured by Douglass (1908) illustrates part of the squamosal in place.

The American Museum collections contain considerable material representing this group of lizards. Skeletal and skull fragments, jaws with teeth, and osteoderms, are included of each of the four genera, *Glyptosaurus* (Eocene), *Xestops* (Eocene), *Helodermoides* (Oligocene), and *Peltosaurus* (Oligocene).



Among nine or more portions of crania collected at various localities only one shows the squamosal arch. This specimen consists of the skull, jaws and scutes of *Xestops* (A. M. N. H. No. 5168) from the Wasatch Eocene of Clark's Fork Basin. The skull has been crushed flat but after preparation indicates the disarticulated bones of the temporal region with remarkable clearness (Figs. 103, 109). Characters seen on this and other specimens which establish distinctions of family rank between this group and the *Helodermatidæ* include:

- (1) Presence of a supratemporal arch and fenestra.
- (2) Separation of prefrontal and postfrontal above orbit.
- (3) Postfrontal and postorbital entirely distinct.
- (4) Pediculate caudal chevrons on the centra (Fig. 101).
- (5) A pineal foramen (very small in *Xestops*, absent in *Peltosaurus*).
- (6) Imbricating osteoderms on the body.
- (7) Teeth on the pterygoid, palatine, and prevomerine bones.
- (8) Parietals united by suture (fused in *Peltosaurus*).
- (9) Transverse processes of first caudal vertebra arising from the entire length of the centrum as in *Gerrhonotus* (cf. Figs. 99–101).
- (10) Jugal with an angular process (Fig. 107).
- (11) Frontals fused (separate in *Helodermoides*?).
- (12) Teeth highly pleurodont with cylindrical, solid shafts and blunt, highly wrinkled crowns, as in some *Anguidæ* (Figs. H and I).

Except for the unfused parietals the above characters would allow inclusion with the *Anguidæ*. There are, however, distinctions which will not permit this:

- (1) The great extent of the patches of teeth on the pterygoids and palatines.
- (2) The massive rectangular jugal, somewhat as in *Heloderma*.
- (3) The extremely large tabulare, exposed dorsally as in *Heloderma*.
- (4) The great length of the slender squamosal which extends forward nearly to the jugal.
- (5) The corresponding reduction of the postorbital.
- (6) The embossed tuberculate osteoderms slightly suggesting *Heloderma* (cf. Figs. 94–98, 104, 105), in ornamentation.
- (7) Quadrate peculiar in having a broad, thin, semicircular internal wing (Fig. 110).
- (8) Lower jaw massive; curved posteriorly as in *Heloderma* (Fig. 106).
- (9) Meckelian sulcus completely covered (Fig. 112).
- (10) Splenial extensive posteriorly (Fig. 112).
- (11) Angular with extensive external surface covering the surangular as a thin plate somewhat as in *Gerrhonotus* (Fig. 107).
- (12) Paroccipital a separate element as figured by Leydig (1872, pp. 26 and 41, Pl. III, fig. 33) for *Lacerta agilis* (Fig. 109).

I think it desirable to reestablish the family *Glyptosauridæ* (Marsh, 1872) to include the genera *Glyptosaurus* Marsh, *Xestops* Cope (for *Oreosaurus* Marsh preoccupied), *Peltosaurus* Cope, *Helodermoides* Douglass, and probably also *Placosaurus* Gervais.



Many of the characters mentioned above indicate that the group is intermediate between the Anguidæ and Helodermatidæ.

Some of the observations of Cope (1884) on *Peltosaurus* may be extended to *Glyptosaurus* and *Xestops*. Thus, in the latter, the premaxillaries are undivided, constituting a separation from the Scincidæ; inferior crests are present on the frontal plate as in *Ophisaurus* and many other Anguimorpha; there is a straight frontoparietal suture and the parietals are extended posteriorly.

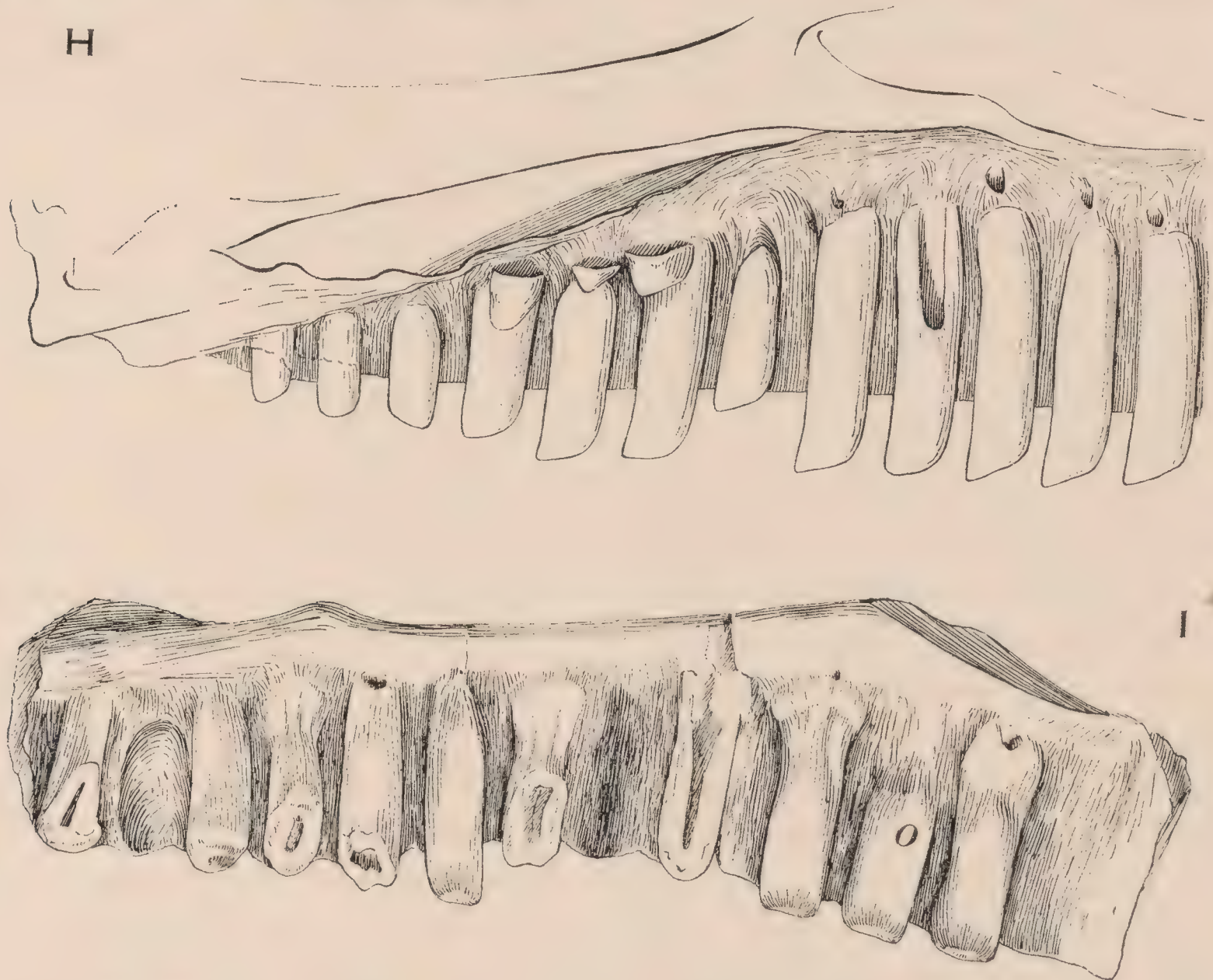


Fig. H. Portion of left maxillary with teeth of *Gerrhonotus scincicauda scincicauda*,  $\times 6$ , A. M. N. H. No. 595.

The small replacement teeth do not enter the bases of the old shafts but lie outside them as in most Anguimorpha. The shafts are semi-solid and chisel-shaped. Similar features are seen in the glyptosaurid, *Xestops* (Fig. I), where an old shaft (O) is seen, which indicates by erosion at the base that a replacement bud has occupied a position comparable with that seen in *Gerrhonotus*.

Fig. I. *Xestops* sp.?,  $\times 1\frac{1}{2}$ , Dept. Vert. Pal., A. M. N. H. No. 5175.

#### Superfamily PYGOPODOIDEA

Vertebral centra short, cylindrical, slightly constricted medially as in the Gekkota; condyles large, nearly as wide as the centra (Fig. 13); ribs with a long, ventral muscular process (Fig. 17); teeth solid; preanal pores present; no Geniomyoideus; no Mylohyoideus anterior superficialis.



This is an isolated group with some apparently primitive features in the vertebræ and throat musculature (p. 370) and with anguroid and zonuroid convergences.

#### Family **Pygopodidæ**

Skull arches both lacking; pleurodont or pleurothecodont; only three or four bones in the mandible (p. 375); no osteoderms; eyelids immobile, transparent; only one series of transverse scales to each body segment; *Rectus superficialis* as in *Chamæsauro* (p. 380).<sup>1</sup>

Jensen (1901), following the suggestion of Boulenger (1885–1887), and after study of additional specimens of the Australian *Ophioseps* Bocage, established the family Ophiopsisepidæ to include that genus. Werner (1912) has referred the form to the Pygopodidæ, a course approved by Fry (1914) and Zietz (1921). Fry evidently considers the genus distinct from *Aprasia* but comparison of Jensen's plate with figures of *Aprasia pulchella* given by McCoy (1885–1890, II, Pl. CLXI, fig. 1) show very close resemblances between the two genera.

*Aprasia* and *Ophioseps* are especially interesting as examples of burrowing forms developed in a limbless family which includes both subterranean and surface-living types. In *Pygopus* and *Lialis* the tail is extremely long and brittle, the ear is exposed and there is no enlargement of the rostral and nasal plates. Although the Horn Expedition Reports state *Lialis* to be a burrower I am assured by Mr. A. S. Le Souëf that the lizard is a surface dweller and that it catches and swallows other surface-living lizards. *Pygopus lepidopus*, from observations of Werner (cited in Brehm's 'Tierleben'), appears to be a climber; the only limbless lizard known to have this habit. *Delma impar* (cf. Lucas and Le Souëf, 1909, p. 219) is probably at least a partial subterranean with much shorter tail and slightly enlarged rostral plate. In *Aprasia pulchella* the tail is still shorter and blunter, the rostrum extended, and the ear completely closed. A specimen is stated by McCoy to have been "turned up by a plough in a field." *Ophioseps nasuta* is a highly specialized pygopodid. According to Jensen's figures the postfrontal is absent and the dentition is reduced to two very small teeth on each side in the extremely weak dentary. The fore part of the skull is expanded as in the burrowing snakes, Typhlopodidæ. The parietals are elongate and fused. *Ophioseps repens* Fry represents the most extreme burrowing habitus developed among the Pygopodidæ with a tail less than a third of

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<sup>1</sup>Peculiar postcloacal bones have been seen in *Lialis* (Fürbringer, 1869). Carlsson (1887) finds them also in *Pygopus* and figures them as furnishing attachment to some of the median subcaudal muscles. There would seem the remote possibility that these bones represent the ossa cloacæ of certain geckos.



the total length and the anterior head plates much broadened. The shoulder girdle has not been investigated.

We should accordingly surmise that the Pygopodidæ are of considerable antiquity, both on account of their morphological peculiarities as a whole and because of the development of a radiation quite unique in a single family of limbless lizards.

The Pygopodidæ have not been found beyond the limits of the Australian-New Guinean-Tasmanian region. Angel (1920) has referred a Siamese genus, *Typhloseps*, to the "Ophiopsisidæ." This lizard appears to be a scincoid possibly near or identical with *Isopachys*, described by Lönnberg (1916) from the same vicinity.

#### Superfamily **ZONUROIDEA**

Vertebræ as in the limbed anguioids; ribs without muscular processes; femoral or preanal pores present; no geniomyoid muscle; no Mylohyoideus anterior superficialis; teeth coelodont; tooth replacement successive. The osteoderms when present are of the highly developed type found in other diploglossids, especially in *Gerrhonotus* and *Ophirosaurus*. The throat musculature, while not primitive, is of a simpler type than in other diploglossids except the Pygopodidæ (cf. Figs. 55-61). Resemblances with the Ascalabota in details of tongue and hemipenial structure, in the pattern of the throat musculature, and in the teeth, are closer than those shown by any other anguimorphs.

#### Family **Zonuridæ**

Skull arches both present; dentition pleurodont; six bones in the lower jaw; interclavicle cruciform with tendency to be widened; osteoderms usually present and non-tuberculate. A rudimentary zygosphenal articulation appears and the skull is roofed over in *Zonurus*. The Geniohyoideus is divided in that genus as in the Iguanidæ. In *Chamæsaurosa*, the Geniohyoideus is not divided and the Rectus superficialis is arranged as in the Pygopodidæ and is free from the skin as in that group; also, as in the Pygopodidæ, there is only one transverse scale row over each segment of the body.

#### DISCUSSION OF THE PHYLOGENY

In attempting to determine the phylogeny, attention has been directed: (1) to the fossil record, (2) to the comparative morphology of the living genera, and (3) to the geographic distribution.

The systematic groups are established primarily on the basis of universally distributed and mutually exclusive characters. The phylo-



geny demands consideration not only of these but of certain archaic features, such as persistence of chorda in the vertebræ, which may be distributed so as to have relatively little systematic value.

In estimating the value of characters supposed to have a bearing on the phylogeny, I have been guided: (1) by the distribution of such characters in paleontological sequences, (2) by the time of appearance in the ontogeny, (3) by the possible vestigial or non-functional nature of the structure in the adult, and (4) by the degree of complexity of the structure, indicating with reasonable assurance whether or not reversion may have taken place. These points are considered in the review which occupies the remaining pages of this paper. The order in which these characters are treated is intended to illustrate the order of their relative phylogenetic importance or PALEOTELIC VALUE. The sum total of such characters in any given form or group is an index of the relative primitiveness, or PALEOTELIC WEIGHT, of that form or group. The approximate PALEOTELIC WEIGHT of each family is illustrated in the phylogenetic chart (p. 333), where the black columns of greatest height indicate the greatest degree of evolutionary development, greatest loss of primitive characters, and the least PALEOTELIC WEIGHT. Such a scale serves as a check, preventing the derivation of any group having a large sum total of primitive heritage from another group with less of such a total.

An example will immediately present itself. Cope (1900, p. 206) derives the geckos (Gekkota = Nyctisaura) from the group to which the iguanids and agamids are referred. By placing the emphasis on the tooth character which Cope has employed this appears plausible, but after comparison of Gekkota and Iguania in total reserve of heritage, such a step seems unjustified (cf. p. 304).

After determining what derivations cannot reasonably be established, I have endeavored to gain some idea of interfamily relationships by examination of characters common to two or more families. This method meets with the usual difficulties that one character may join, let us say, families A and B, another A and C, and another B and C, leaving us as much in the dark as before concerning the true descent. Consequently, where there is conflicting evidence, an attempt has been made to find two or more characters of practically universal distribution among the groups in question. This procedure has been adopted for still higher groups, with results as indicated in the accompanying chart.

Another line of evidence which cannot well be set aside is the matter of distribution (cf. Gadow, 1901; Palacký, 1899). In some cases this



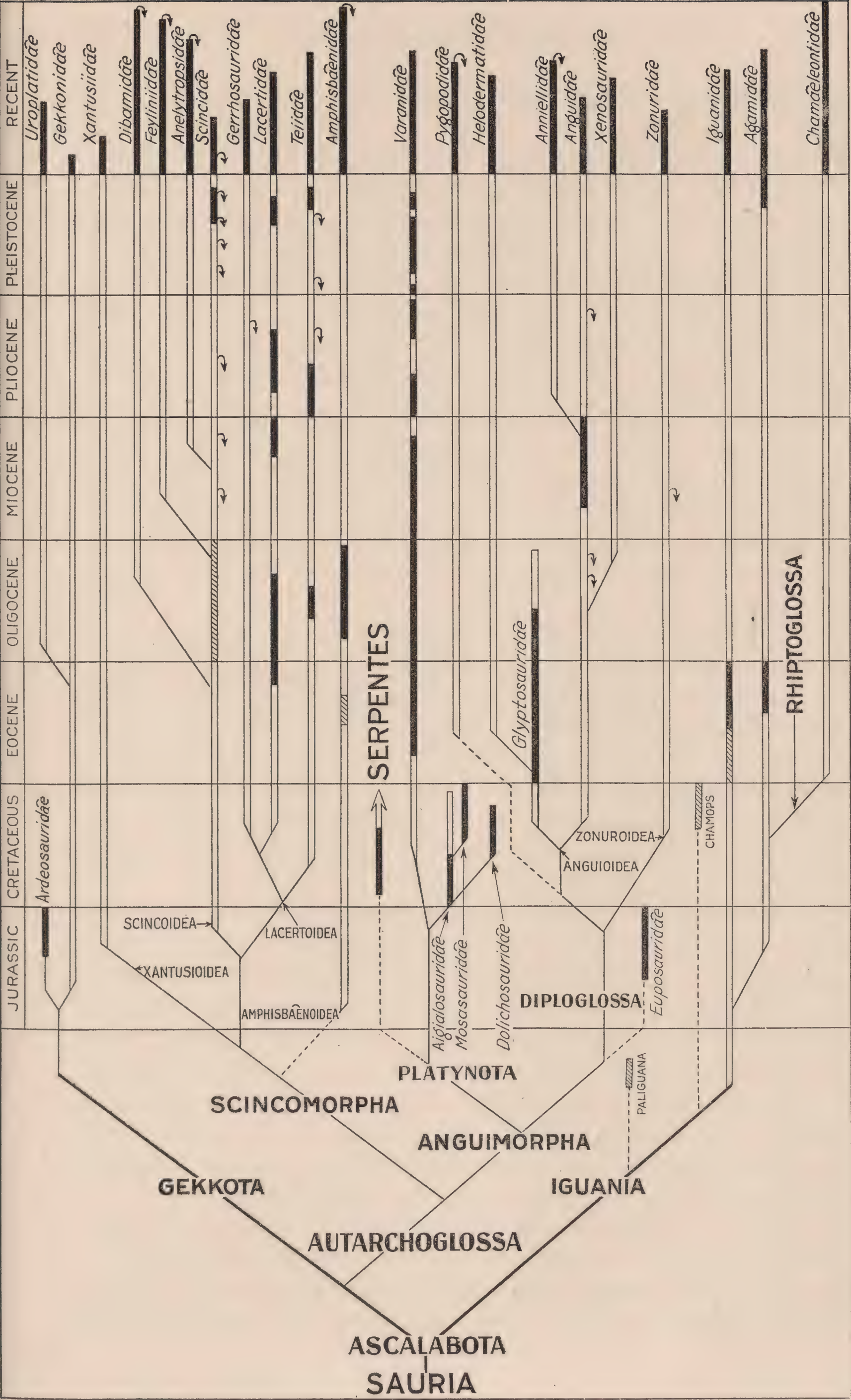


Chart Illustrating the Phylogeny and Classification of the Families of Lizards.

Heavy black columns under the space marked "Recent" indicate the relative specialization of each family. Retention of primitive characters and paleontological weight is greatest in those groups having the lowest columns. The fossil record includes only well authenticated genera (heavy black) and fairly certain (cross-lined) references. Many fossil genera are omitted altogether as of unsatisfactory status. Dotted lines denote uncertain relationships; downwardly directed arrows, limbless families and groups of species.



gives important supplementary data as to the relationships and antiquity of groups.

Most of the "primitive" families (here so called) are of wide distribution. The Gekkonidæ and Scincidæ are cosmopolitan. The Anguidæ holarctic and South American. The Iguanidæ are scattered, related forms) cf. p. 308), occurring in Madagascar, the Fiji and Friendly Islands, and the Western Hemisphere. Supplantation of this group by the Agamidæ has doubtless occurred in most parts of the Old World. The Amphisbænidæ, known abundantly from the Oligocene of temperate North America, occur at present throughout the tropics except in Australasia, most Oceanic Islands, the Oriental region, and Madagascar. The Amphisbænidæ, distributionally an ancient group, have acquired an extreme degree of specialization, obscuring much of what appears to have been a relatively primitive heritage. Other groups have the distributional facies of relicts—the Helodermatidæ in Borneo and southwestern America,—the Xantusiidæ in southwestern America and the West Indies.

Some families of seemingly intermediate age on the basis of structure are restricted to the Old or New World exclusively, such being in the Old World: the Gerrhosauridæ (Africa and Madagascar); Lacertidæ (Africa and Eurasia); Varanidæ (tropical Asia and Australasia, and Africa); Zonuridæ (southern and eastern Africa); Agamidæ and Chamæleontidæ (Africa, Madagascar, and southern Asia, eastward into India); and the Teiidæ in the New World. Boulenger (1920) expresses the possibility of derivation of the Lacertidæ from unknown Old World teiids and subsequent supplantation of the latter.

Three of the more recent families occurring in Asia are absent from Australia—Lacertidæ, Anguidæ, and Chamæleontidæ. Those absent from Madagascar but occurring in Africa are the Lacertidæ, Varanidæ, Anguidæ, Zonuridæ and Agamidæ. Many locally distributed families are presumably so because of recent origin. We might place in this category the Uroplatidæ, possibly derived from less specialized geckos in Madagascar; the local, burrowing scincoids, independent families of which seem to have arisen in Mexico, in Africa and in the East Indies; the burrowing anguroid, *Anniella*, of California; the non-primitive Xenosauridæ of extremely local central Mexican distribution.

Temperature exerts an important control over the distribution. Anguids are rare in the tropics but range far northward and higher in the Alps and the Sierra Nevada than other lizards. The varanids, geckos and gerrhosaurids are tropical and subtropical. The amphisbænids



are almost exclusively tropical—partly, perhaps, because of soil conditions or food supply.

What appear to represent archaic members of primitive groups (*Phyllurus* and *Nephrurus* among the Gekkonidæ, and *Trachysaurus*, *Tiliqua*, and *Egernia* among the Scincidæ) occur in Australia. The New Zealand geckos, *Naultinus* and *Hoplodactylus* are perhaps primitive in the arrangement of the femoral pores. Other cases of peripheral distribution of ancient forms (cf. Matthew, 1915, pp. 288–292) are rare. The recent African range of *Nucras*, a generalized lacertid, also found in Oligocene Amber of Prussia, is significant (cf. Boulenger, 1920); also the African and Australian dispersal of primitive anguimorphs, the Zonuridæ and Pygopodidæ.

After trying to establish the relationships on the basis of universally distributed characters, it has proved instructive to ascertain the “tendencies of evolution” among the chief groups. Some of these apparent tendencies are listed in the sections devoted to group characters, and the matter deserves remark.

I have divided the Sauria into two main divisions partly on the basis of the presence or absence of an extensive muscle—derived from the Rectus and frequently connected with the ventral scales,—partly on certain hemipenial characters worked out by Cope thirty years ago and used by him in the definition of less extensive groups, and partly on characters of lepidosis. In the Ascalabota the muscle in question is absent and no other muscles take its place. In all limbed Autarchoglossa, it is present. In all Ascalabota, which includes about half the known species of lizards, no snake-like or limbless forms of any kind are developed. Among the Autarchoglossa, limbless or practically limbless forms are present in no less than ten different families. Apparently a latent “tendency” is here present which may be preserved under certain requirements of habitat. This particular “tendency” is correlated with the presence of a certain muscle. The muscle seems to be useful in pulling the body over the ground as the limbs cease to be functional. To take another case: many permanently arboreal lizards are developed among both of the divisions just considered. In the Autarchoglossa not a single arboreal form shows any pronounced modifications in body form or in the shape of the digits. K. P. Schmidt has illustrated (1919, Pl. XXIII, fig. 2) an African bark-living lacertid (*Holaspis*) that has gained a slightly flattened form and Boulenger (1917, p. 232) describes another lacertid (*Platyplacopus*) which has developed specialized distal phalanges probably in correlation with the habit of living in the tops of tall grass.



But these are minor matters in comparison with the profound changes which accompany permanent arboreal life among the Ascalabota. Here we have the following conditions. Arboreal Gekkota, which are usually bark-dwelling and cling close to the broader surfaces of trees, often exhibit unusually flattened bodies and sometimes have lateral fringes and webbed feet; truly compressed forms are unknown in this group. The permanently arboreal Iguania are all compressed and this condition is carried to an extreme in the *Rhoptoglossa*. *Draco* is slightly depressed but here is a volant as well as arboreal habitus. Both the Gekkota and the Iguania develop laminate sucking digits—the arboreal *Autarchoglossa* never develop them. The histology of these structures is similar in the two groups of Ascalabota.

The chart (p. 333), is intended to exhibit the phylogeny as far as the various families. The conventional synopsis of classification is usually thought of as being dichotomous. A true phylogeny is of course not necessarily so. It might be considered undesirable to give equal rank to subdivisions such as the *Autarchoglossa* and *Ascalabota* where one group is apparently derived from the other and not from a common stem. The same argument would hold for the *Serpentes* and *Sauria*, and for the *Rhoptoglossa* and *Iguania*. It is obvious that groups held to be equal or dichotomous on the basis of classification may not have had an equal extent of geologic history, and when it is intended to illustrate this history simultaneously with the classification some difficulties present themselves. The agreement between classification and phylogeny is seldom exact and allowances must be made for artificiality on both sides.

It may also be objected that in the chart the *Iguania* are more widely separated from the *Gekkota* than their order in the synopsis would indicate. This difficulty will be avoided if one thinks of the chart as rolled into a cylinder with the main stem of the *Iguanidæ* near that of the *Gekkonidæ*. The linear arrangement of the families is intended in some degree to express relationships which cannot be shown in the branching scheme.

Thus in the linear arrangement, the *Xantusiidæ* are placed near the *Gekkonidæ*, to which they show some affinity, and in the branching scheme they retain their place among the *Scincomorpha*, where the greater number of their characters would place them. So also the *Zonuridæ* occupy a position next to the *Iguanidæ* on the basis of common retention of certain characters.

The extent of the paleontologic record is indicated in black. The almost continuous record of the rather specialized *Platynota* far into the Cretaceous forces us to extend many of the other less specialized



groups back to beyond this point. There are no records of true Sauria from the Permian but the supposedly ancestral form *Aræoscelis* is known to be of that age. The Sauria constitutes an entirely natural and diversified group and appears to have arisen in the Permian from a stem perhaps related to Williston's *Aræoscelis*. This ancestral form should have a fair proportion of the following characters:

Vertebræ with centra cylindrical, not tapering, biconcave, and with thin, half ring-shaped intercentra.

Teeth thecodont or pleurothecodont.

Postfronto-squamosal arch short and massive. Postfrontal and postorbital present.

Postorbital arch (jugal) broad, short, and erect. Skull elevated.

Two dorsal temporal elements adjoining the quadrate.

Median bones of skull-roof not united.

Teeth present on the pterygoid, palatine, and vomerine bones.

A parasternum.

A proatlas (?).

An os intermedium.

A pineal foramen.

Pterygoids separated on the mid-line.

Ribs slightly double-headed. The third cervical with ribs.

Lacrymal exposed externally as part of lower anterior border of orbit.

Scapula narrow at base.

Coracoids plate-like and shallowly emarginate anteriorly.

Clavicle broadened toward the mid-line.

Interclavicle a subrhombic plate.

An epipterygoid.

Osteoderms, if present, compound or diffuse.

#### EVALUATION OF PALEOTELIC CHARACTERS

An attempt has been made to assign some comparative rank (paleotelic value) to each of the following characters, those first treated being thought the older, hence the more important in determination of the phylogeny. A form having even a few characters of high antiquity may be considered more ancient than one having many characters of lesser paleotelic value. High specialization in a group may obscure an archaic position that can only be traced by recognition of satisfactorily primitive characters. By employment of such a scale as here introduced, an estimate of the PALEOTELIC WEIGHT of various groups may be ascertained. By such an estimate we may detect, even in the presence of secondary specialization, the relative antiquity of highly modified forms. The characters enumerated are subsequently discussed following the order of the list which is intended to indicate their relative phylogenetic value, assigned after consideration of the points mentioned in the preceding section.



- 1.—Three complete branchial arches.
  - 1a.—Some remnants of third arch remaining.
- 2.—Vertebræ amphicœlous.
  - 2a.—Procoelous condyle small.
  - 2b.—Zygosphenal and zygantral articulations not developed.
  - 2c.—A continuous series of half-ring-shaped free intercentra in cervical and dorsal region.
  - 2d.—Intercentra persistent but fused to the procoelous condyles.
3. Two complete skull arches.
4. Os tabulare (Williston) present.
5. Pentadactyl limbs and girdles complete.
  - 5a.—Eyes well developed and with sclerotic plates, eyelids free.
- 6.—Lungs equally developed on both sides and simple.
- 7.—Premaxillaries, nasals, frontals, and parietals unfused.
- 8.—Prevomerine bones paired.
- 9.—Hemipenes not flounced or laminate.
10. Third cervical vertebra with ribs.
- 11.—Postfrontal present.
- 12.—Lacrymal present.
- 13.—Pleuro-coelo-homodont dentition.
- 14.—Teeth present on palate.
- 15.—Rhomboid or cruciform interclavicle.
- 16.—Expanded non-perforate clavicle.
- 17.—Mylohyoideus anterior in one layer, with many regularly spaced interdigitations with the Geniohyoideus, and scarcely separable from the Mylohyoideus posterior.
- 18.—Tongue broad, fleshy, and smooth or papillate.
- 19.—Six separate elements in lower jaw.
- 20.—Caudal chevrons attached intercentrally.
- 21.—Os intermedium present and separate in the carpus.
- 22.—A Rectus lateralis present.
  - 22a.—A parasternum.
- 23.—Epipterygoid (*Columella cranii*) present.
- 24.—Pterygoids separate.
- 25.—Pineal foramen present and located between the parietals.
- 26.—Osteoderms compound.
- 27.—Several rows of belly scales over each body segment; sometimes with a few larger dorsal tubercles.
- 28.—Proximal belly of Biceps brachii simple.
- 29.—Skull elevated.
- 30.—Os hypoischium not present.
- 31.—No bony patellar sesamoids.
- 32.—Sternum without fontanelles.
- 33.—Scapulo-coracoid emarginations and fenestræ present.
- 34.—No endolymphatic sacs.

I have reviewed the distribution of each character discussed in order to bring out systematic points and to indicate the gaps in our knowledge.



## 1.—THE BRANCHIAL ARCHES

Cope (1892) was the first to point out the significance of modification of the branchial arches among lizards. Sauvage (1878), Parker (1880), and Van Bemmelen (1887) made pioneer discoveries. Supplementary work has been done by Gaupp, Gadow (1888), Beddard (1905*b*, 1907), Zavattari (1908), Fürbringer (1919), Hewitt (1920), and Noble (1921). I have examined twenty-six genera in various families (Figs. 27–38).

*Coleonyx* (Gekkonidæ) is the only genus so far known in which three complete arches still persist (cf. Fig. 27; Cope, 1892, Fig. 7 [Fig. 8 erroneous]; Noble, 1921, Fig. 3A). The third arch here appears to be functionless, being unconnected with the muscles in its dorsal half (second epibranchial) and lying as a thin flexible cartilage just dorsal to the muscles, Sternohyoideus and Constrictor colli. The second ceratobranchial is attached to the dorsal surface of the Sternothyreoideus.

In most lizards the third arch has been either entirely lost or is well reduced. A few geckos (*Lepidoblepharis*, *Gonatodes*, *Lathrogecko*, *Psilodactylus*) and xantusids (*Xantusia*, *Lepidophyma*) have the third arch nearly complete, with only a slight break between the two halves.

Both second epibranchials and second ceratobranchials are said or known to be present in the following genera:

Gekkonidæ: *Coleonyx* (2 species), *Sphærodactylus*, *Lepidoblepharis*, *Lathrogecko*, *Gonatodes*.

Iguanidæ: *Iguana* (some others according to Fürbringer).

Agamidæ: *Uromastix* (some others according to Fürbringer).

Xantusidæ: *Xantusia* (2 species), *Lepidophyma*.

Lacertidæ: *Nucras*, *Lacerta*, *Algiroides*.

Scincidæ: *Trachysaurus*, *Tiliqua*, *Egernia*, *Scincus*, *Lygosoma*, *Eumeces*, *Macroscincus*, *Chalcides*, *Liolepisma*, *Mabuya trivittata*.

Zonuridæ: *Zonurus*, *Pseudocordylus* (?), *Chamæsaura*.

The second epibranchial is apparently absent and the second ceratobranchial is still present in the following:

Gekkonidæ: *Aristelliger*, *Platydictylus mauritanicus* (Ficalbi, 1880).

Iguanidæ: Most of the genera, including *Chalarodon*.

Agamidæ: Most of the genera (absent in *Amphibolurus*, rudimentary in *Chlamydosaurus*, Beddard, 1905*b*).

Teiidæ: *Bachia intermedia*.

Amphisbænidæ: *Chirotes*, *Amphisbæna*.



In the arboreal iguanids and agamids this section of the arch plays an important role in the support of the throat fan and is sometimes greatly elongated (cf. Bell, 1825 and von Geldern, 1919).

The second epibranchial is present and the second ceratobranchial is absent in the following:

Gekkonidæ: *Homopholis*, *Pachydactylus*, *Platydictylus guttatus*.

Uroplatidæ: *Uroplates fimbriatus*.

Gerrhosauridæ: *Gerrhosaurus* (3 species), *Zonosaurus*.

Teiidæ: *Tupinambis*.

Helodermatidæ: *Heloderma*.

Anguidæ: *Gerrhonotus scincicauda*.

All traces of the third arch are lost in:

Gekkonidæ: *Paragonatodes*, *Hemidactylus*, *Gehyra*.

Pygopodidæ: *Lialis*, *Pygopus*.

Chamæleontidæ: *Chamæleon*.

Scincidæ: *Acontias*.

Feyliniidæ: *Typhlosaurus*.

Dibamidæ: *Dibamus* (hyoid arch also wanting).

Amphisbænidæ: *Rhineura*.

Varanidæ: *Varanus*.

Anguidæ: *Ophisaurus*, *Anguis*.

Xenosauridæ: *Xenosaurus*.

Anniellidæ: *Anniella* (hyoid arch also totally wanting).

Extreme reductions are found in the terminal and specialized forms of the phyletic system.

The degree and point of attachment of the third and first arches to the skull may be of some significance but the circumstances are not all clear. There appear to have been migrations of the point of contact.

The second epibranchial is connected with the skull in the most primitive forms,—*Coleonyx* and many other Gekkonidæ, *Uroplates*, *Xantusia*, *Lepidophyma*, *Trachysaurus*, *Gerrhosaurus*, and *Gerrhonotus*—being attached to the paroccipital in *Coleonyx* and *Thecadactylus*, in *Gonatodes*, *Lepidoblepharis*, *Lathrogecko*, *Sphærodactylus*, and *Lepidophyma*, and to a tubercle on the exoccipital in *Trachysaurus*, *Tiliqua*, *Egernia*, and *Gerrhosaurus*.

Attachments of the hyoid (first arch) to the skull are known in a number of ascalabotids, in *Gerrhosaurus*, *Lacerta* and *Gerrhonotus*, and possibly in *Amphisbæna*. The latter case depends upon interpretation and may be left for the moment in order to follow the ontogeny of the



hyoid as investigated and reviewed by Versluys (1898 and 1904, cf. Gregory, 1913).

The reptilian ear bones (columella auris), consisting of the stapes and extra-columella and the various parts and processes appertaining thereto<sup>1</sup> have usually been considered as modifications of the cervical extremity of the hyoid arch. This derivation has been traced in embryos of *Sphenodon* (Howes and Swinnerton), in *Sceloporus* (Kingsley), in *Gekko verticillatus*, *Platydictylus mauritanicus*, and *Lacerta agilis* (Versluys, 1904). Rice (1920) explains that "the preponderance of evidence strongly favors the interpretation of the columella as a unit structure with otostapes and hyostapes in direct genetic relation to one another . . . that the otic capsule, columella auris, and hyoid arch are all parts of a 'continuous stroma' of undifferentiated early embryonic tissue." The primary relation of the tip of the hyoid to the ossicula auditus becomes modified in the adult form in primitive lizards by dorsal migration or looping of the remaining portion of the hyoid extremity which finally forms a close union with the paroccipital process of the opisthotic bone. This post-primary cervical union occurs only in certain ascalabotid lizards and in *Sphenodon*. It is known in many geckos including *Coleonyx* (2 species), *Gekko verticillatus*, *Platydictylus mauritanicus*, *Pachydictylus bibroni*, *Uroplates fimbriatus*, *Uromastix spinipes*, and *U. acantherinus* (cf. Versluys, 1898, Figs. 5, 6, 8, 18, and 23). It represents a stage of evolution in which the primary connection of hyoid with extra-columella has just been lost. Its ontogenetic similarity in the Gekkota and in *Uromastix* is strengthened by the presence and attachments of the Stylohyoideus. This muscle (cf. Versluys, 1898, Figs. 9, 15, 17, and 23), morphologically a part of the posterior edge of the Mylohyoideus posterior, arises from the extremity of the epihyal. Its embryology in geckos shows that the fundamental origin is upon the tip of the epihyal where the latter joins the interhyal cartilage. When the epihyal moves dorsalwards to reach the paroccipital process the muscle is carried with it finally to arise in this unusual position.

In *Lacerta agilis* and other autarchoglossids (cf. Versluys, 1904, pp. 132, 133) there is no stylohyoid muscle. The epihyal does not lose its connection with the elongate interhyal and a ligament comes to take the place of the latter establishing a loose connection with the paroccipital process, a union which persists into post-embryonic life. The condition in the Ascalabota is more primitive than the union found in *Lacerta*

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<sup>1</sup>Versluys finds that in geckos the foot plate develops independently of the capsule, but as a part of it in other lizards.



*agilis*. *Gerrhosaurus zechi* (Fig. 32) has a closer union than *Lacerta*; *Gerrhonotus* has a loose connection. *Amphisbæna* has been said to have a persistent connection of the hyoid with the skull. This is a matter worthy of attention.

The conditions found in the Amphisbænidae are most anamalous (cf. Versluys, 1898, Figs. 66, 68, and 69). In *Amphisbæna alba* (A. M. N. H. 8747) an extremely long, cartilaginous rod-like "extra-columella" lies in articulation with a short, relatively broad and mobile stapes and runs forward across the quadrate in a deep groove to the labial side of the dentary as far as the region of the submaxillary gland. If this element represents the epihyal, as Fürbringer (1919) would have it, the Amphisbænidae retain the most primitive connection known in adult reptiles. This view, as Versluys himself grants (1904), is open to considerable doubt.

I have found an "extra-columella," undoubtedly homologous with that noted by Versluys, in *Amphisbæna fuliginosa*, in *Rhineura floridana* and in the unhatched embryo of *Amphisbæna cæca*. In *Rhineura* the element is bony, and very much shorter than in *Amphisbæna* (cf. Figs. F, G, and Versluys, *loc. cit.*). It fastens to the expanded distal extremity of the elongate stapes by strong ligaments and lies imbedded in the handle of a Y-shaped fascia running beneath the rictus to the areas of spongy tissue under the upper and lower lips. It is so arranged that vibrations received through this tissue must be transmitted directly to the mobile stapes. It might be considered simply as an enlarged extra-columella functioning in an unusual way in absence of a tympanum.

In an embryo of *Amphisbæna cæca* (Fig. F) the extra-columella is enormous, extending as a thick cartilaginous band, in the position of the rod-like structure of *Amphisbæna alba*, forward to the spongy tissue beneath the lower labials. The union with the abbreviated stapes is a mobile articulation and a small cartilaginous element (Fig. F, *Otostp.*) is intercalated. This nodule would represent the outer segment of the so-called otostapes of normal lizards (cf. Versluys, 1904, Fig. 10) if we could consider the elongate external rod as a true extra-columella.

What is the evidence in favor of such a view? (1) No connection of any kind was observable in our embryo between the extra-columella and the process representing the hyoid (first arch). (2) A true ceratohyal is present in this embryo (Fig. F, *ceratohy.*) in the position occupied in the Teiidae. The main portion of the hyoid in adult amphisbænians seems to represent the elongate process of the basihyal of the teiids. (3) This small ceratohyal in normal posterior position would presum-



ably never have had a connection with the forward tip of the extra-columella as would be necessary on the supposition that the extra-columella is a remnant of the epihyal. Such a connection would be unlikely owing to relations of neighboring muscles and ligaments. (4) The extra-columella in *Rhineura*, although bony, is of much more typical extra-columellar form and would scarcely be mistaken, as the homologous rod-like element in *Amphisbæna* has been, for a part of the undifferentiated epihyal. The outer ear of amphisbænians is not a degenerate structure but a highly specialized one in which the extra-columella transmits vibrations from the side of the head and lower jaw instead of from the tympanum in the usual way. This may account for the extraordinary change in the form of the extra-columella and indicate that we are not dealing with a part of the hyoid in such an exceedingly primitive and unsaurian position.

## 2.—SAURIAN VERTEBRÆ

What appears to be the most primitive type of vertebral column found among the Sauria occurs in many of the Gekkota (e.g., *Gekko verticillatus*, *Phyllodactylus*, *Pachydactylus*, *Hemidactylus*, *Tarentola*, *Gehyra* and *Uroplates* (cf. Siebenrock, 1893). Here the centra are biconcave and the cervical intercentra (hæmopophyses) are similar to and directly continuous with the intercentra of the dorsolumbar region as far posteriorly as the sacrum (cf. Baur, 1886a). The intercentra including those of the atlas and axis vertebræ are thin, half-ring-shaped bones (cf. Figs. 1-2) usually separate from the centra (quite strongly fused in *Thecadactylus rapicauda*), and furnishing attachment for the long subvertebral ligament and some of the subcervical axial musculature. The conditions are similar to those found in *Aræoscelis*, *Sphenodon*, *Dimetrodon*, *Trimerorhachis*, *Seymouria*, and many other primitive reptiles. All lizards except the amphiœlous gekkonids have procœlous vertebræ.

The transition from amphiœlous to procœlous conditions involves no profound change. Early stages in procœlous lizards are similar to those in amphiœlous geckos and in *Sphenodon*, and somewhat different from crocodile (Goette, 1894). In the adult the chief difference, according to Goette, between the amphiœlous geckos and the procœlous lacertids and anguids is that in the former the intervertebral rings do not entirely pinch off the chorda (cf. also Schauinsland, 1906).

Goette (1894, 1897) did not recognize the importance in geckos of the intercentrum, which was discovered later by Baur. The differences



between procœlous and amphicœlous geckos probably include the elimination of the intercentral chorda by the constricting and thickening of the intervertebral disc which becomes reduced, rounded, and attached anteriorly to form the small condylar ball. The condyles fuse ventrally with the intercentra, which, in higher forms, become indistinguishable. The subvertebral ligament comes to insert at the point of fusion of each intercentrum with its condyle. In the procœlous gecko, *Coleonyx variegatus*, and in *Xantusia vigilis* (cf. Figs. 4 and 8), the intercentra may still be found as fused, bony, scale-like elements, and the centra are like those of amphicœlous geckos except for the development of a cup-and-ball articulation.

Noble (1921), in a discussion of the relationships of certain groups of geckos, considers the amphicœlous condition as primitive on comparative grounds. *Aræoscelis*, a supposed Permian ancestor of the Squamata, has amphicœlous vertebræ not unlike those of the geckos, with "persistent intercentra" (Williston, 1914, Fig. 1 and manuscript).

The degree of enlargement and specialization of the procœlous condyle is an important index of the amount of specialization in the various families (Figs. 1-26). The initial advance from the most primitive gekkonid condition is seen in the lower iguanid and scincomorph genera. The amphisbænids are similar to *Ophisaurus* and the Eocene varanid *Saniwa* in broadening of the condyle; while the most advanced saurian stage is seen in the Pleistocene and recent Platynota where the extremely large condyles are set off by a waist-like constriction of the centrum. A sharp flange is raised at the periphery of the flattened articular surface and that surface itself is turned dorsally so as to be almost concealed in direct ventral view.

In the chameleons and pygopodids, special developments are indicated (cf. Figs. 7, 13 and 17). The latter retains gekkonid characters, apparently, in the broad, squarish, ventral outline, the median constriction of the centrum, and the persistence of well-developed subcentral foramina in the median position. The large condyle would indicate a position well above that of the modern geckos. The chamæleontid type is elongate, narrow and cylindrical.

The size of the intervertebral canals, large in the Gekkota and Xantusiidæ, undergoes reduction in the more advanced groups. The paired subcentral foramina, present in geckos, pygopodids, and amphisbænians (cf. Figs. 1-4, 8, 9 and 13) appear less frequently among the Scincomorpha and are absent in the higher anguimorphs and in the chameleons.



Some families develop a zygosphenal articulation supplementing the ordinary zygapophyseal type. Although this supplementary articulation is characteristic of snakes it occurs, so far as I know, in no snake-like lizard. It is present in the large iguanids, including *Dipso-saurus* and *Sauromalus*, and, as a rudiment, in *Crotaphytus* (cf. Cope 1892, pp. 199–209). It is known to be absent in the iguanids, *Anolis*, *Polychrus* (Boulenger, 1891a, p. 113), *Sceloporus*, and *Phrynosoma*. It is present among the Lacertidæ and Teiidæ (large in *Tupinambis*; absent or extremely rudimentary in *Bachia*); and occurs among the Varanidæ in the Megalaninæ and in the North American Eocene genus *Saniwa* where it is small. It is present among the Mosasauridæ and Dolichosauridæ. It is small in *Zonurus*.

Development of the zygosphene and zygantrum appears to be a result of enlargement of the bony area of the vertebræ, and especially of the forward part of the neural arch, until interference with the base of the arch of the next forward vertebra takes place.

Boulenger, largely on the strength of this character, suggests placing *Thinosaurus*, of the North American Eocene, with the Teiidæ and not with the Varanidæ. Other characters of the vertebræ of *Thinosaurus* and the related *Saniwa* indicate varanid relationships. (Cf. Figs. 23–26.)

Presence of zygosphene and zygantrum alone cannot be taken to show affinity with the serpents. Secondary formation seems to be the rule.

### 3.—THE SKULL ARCHES

Two normal skull arches (cf. Figs. 106–108) are present in all non-burrowing forms with the exception of the Gekkonidæ and Uroplatidæ, the Varanidæ, the Pygopodidæ and the Helodermatidæ. It is not possible to account for the loss of arches in these families on adaptational grounds.

In all permanently subterranean forms the head becomes bullet-like, with partial and often total loss of arches and more solid union of other skull elements. This occurs in all the limbless autarchoglossid burrowers but not in the limbless grass-living members of the same group, including the scincomorph *Tetradactylus*, the anguimorphine *Ophisaurus*, *Anguis*, and *Chamæsauro*.

The relationship of the Squamata to other orders of reptiles and especially to the Rhynchocephalia is a problem intimately concerned with the correct identification of the bones of the temporal arches. The homologies in lizards and *Sphenodon* of the four elements of the cotylosaurian skull, lying in the temporal region above and lateral to the



quadrate, have been variously interpreted and speculated upon; yet no concord is in sight as to what the two elements usually present in lizards really are.

Baur (1889), Williston (1914), and Watson (1914) essentially agree that the streptostylic condition of the Squamata arose not from the "diapsid" modern Rhynchocephalian by dropping out of the lower arch but by emargination from the ventral side of a broad, unfenestrated lateral arch or plate. The presence of a quadratojugal embryonic connection (cf. Broom, 1903*b*) is not at present regarded as strong evidence against the emargination hypothesis. Baur could show no very convincing evidence for his view. Watson regarded the condition in *Pleurosaurus* as ancestral. In *Pleurosaurus* the postorbital (= ? postorbital + postfrontal) is massive and in connection with the jugal extends posteriorly to form a broad lateral temporal arch, unfenestrated and scarcely emarginate below. A small quadratojugal and "squamosal" are present in about the position seen in *Sphenodon*.

Watson thinks it possible that the quadratojugal in the primitive state, such as in *Pleurosaurus*, could have retreated upwards as emargination progressed and the quadrate became free. The "*Pleurosaurus* theory" would leave us with an outer quadratojugal and an inner squamosal in the typical lizard. One chief objection of course is the late geologic occurrence of the "Acrosauria" including *Pleurosaurus*, and the fact that highly developed true lizards (Euposauridæ) occur with them in the Jurassic. Another difficulty is the wide difference between the appearance of the quadratojugal in the primitive state, in Cotylosaurs, Pelycosaurs, and in *Pleurosaurus*, as a lower lateral element, and the supposed "quadratojugal" of lizards, an upper lateral bone often with a strong process reaching the parietal, and with practically no extension downwards over the quadrate.

#### 4.—THE TABULARE QUESTION

Williston (1917, p. 68 and manuscript) believes that the Squamata arose at an earlier date than the Rhynchocephalia, and without close relationship to that group, from forms represented in the Lower Permian of Texas by his genus *Aræoscelis* and possibly also by *Kadaliosaurus* Credner (1889). The forms represented by *Aræoscelis* are described as "very slender, arboreal or leaping, hollow-boned reptiles. . . . The broad temporal region is formed apparently of a single bone, here identified as the squamosal. The quadrato-jugal is absent. The dermo-supra-occipital is apparently large. [Tabulare present.] Lacrimal vestigial or



absent. A parietal foramen. All cranial bones paired. Palatal bones with teeth. . . .Vertebræ amphicœlous with persistent intercentra. Cervical ribs, at least, single headed, the dorsal more or less dichocœphalous. Coracoid and scapula closely fused. Humerus with both entepicondylar and ectepicondylar foramina, . . . the earliest definitely known reptile with a single upper temporal vacuity, bounded as in lizards, and a fixed quadrate." (Cf. Williston, 1914.)

Williston (1917, p. 66) derives the Squamata with the Ichthyosauria directly from the Cotylosauria and unites the two former under the name Parapsida because of supposed similarity of origin of the temporal openings in these orders. The upper temporal fenestra he believed to have arisen "by the primitive separation of the postorbito-squamosal arcade from the parietal" and the lower fenestra, by emargination of the squamosal, from a condition such as that seen in *Aræoscelis*. An important point is that in the Parapsida "an additional temporal bone was retained long after it was lost in other [reptilian] groups." This is the so-called tabulare present according to Williston in some lizards, in the Ichthyosauria, and in *Aræoscelis*.

In *Aræoscelis*, what is considered to be the tabulare, forms the posterior boundary of the superior temporal opening and lies superficially between the squamosal, parietal, and paroccipital, adjoining also the antero-dorsal end of the quadrate. Few would question this homology, but the identity of the true tabulare with the inner temporal bone in lizards is a contention which only Williston and Broom (1913) have been bold enough to support.

The relations of the inner element to adjacent parts in lizards, mosasaurs, ichthyosaurs, and other forms engaged Baur (1886*b*, 1889, 1892, 1894, 1895, 1896) and Cope (1895*a*, 1895*b*, 1896) in a long controversy. Baur (1886*b*, 1886*c*) originally regarded the outer element in lizards as the squamosal, the inner as the supratemporal. In 1889 he considered the outer to be the quadratojugal and the inner the squamosal. The single element present in geckos he thought represented the quadratojugal (1889). Later (1894) he further modified the terminology calling the upper outer element the prosquamosal because of confusion in the employment of the term supratemporal and restricting the quadratojugal to the lower outer element not considered as present in the Sauria.

Cope stoutly maintained his view that the inner element represents the paroccipital, a bone which has been shown (Leydig, 1872) to be separately present in certain forms along with Cope's "paroccipital." Cope (1895) calls the outer element of lizards the supratemporal and



believes it to be homologous with the similarly placed (median) element in ichthyosaurs. The lower outer element (quadratojugal of Baur) in ichthyosaurs and *Sphenodon* he terms the zygomatic.

Beddard (1905a) notes the presence of still a third "bone" adjoining the end of the paroccipital process of certain lizards (*Uromastix*, *Lacerta*, *Heloderma*). He calls this supratemporal 2. Fortunately "supratemporal 2" has been long since disposed of by Versluys (1898, 1904) who shows it to be essentially a cartilaginous epiphysis on the tip of the paroccipital process formed partly *in situ* and largely from the columellar and epihyal cartilages which extend dorsally to form paroccipital connections that persist in certain forms (cf. p. 341). Versluys notes the "epiphysis" in the Gekkonidæ and in *Uromastix*, *Agama*, *Calotes*, *Amphibolurus*, and *Draco*; in *Iguana*, *Phrynosoma*, and *Polychrus*; in *Trachysaurus*, *Gerrhosaurus*, *Tupinambis*, *Heloderma*, *Varanus*, and *Zonura*. It appears to be absent in *Mabuya*, *Lygosoma*, *Ophisaurus*, and *Anguis*.

It might appear profitable to compare the conditions in lizards with those found in ichthyosaurs and especially with the thalattosaurs. Unfortunately, the temporal region of the latter is still imperfectly known. In *Thalattosaurus alexandræ*, Merriam (1905) regards two temporal elements as questionably present and calls the inner one the squamosal, the outer prosquamosal. The relations appear similar to those of lizards if we accept von Heune's view of the matter (1910a, 1912). Merriam did not succeed in discovering the quadratojugal but thought he could see indications of its presence. Von Heune apparently favors omitting the quadratojugal, and thinks he can recognize in the temporal region an outer "squamosal" (prosquamosal of Merriam), an inner supratemporal, and an element lying between the two which may represent a backward prolongation of the very large postfronto-orbital or a part of the supratemporal (=squamosal of Merriam).

It would seem very highly improbable to say the least that the outer dorsal element ("prosquamosal") in thalattosaurs can represent the quadratojugal, as would be necessary on Watson's view, providing the thalattosaurs are streptostylic. If they prove to have a lower quadratojugal it would be impossible for the upper bone to represent that element, and this makes it seem that in either case the "*Pleurosaurus* theory" as far as it relates to the quadratojugal is untenable.

In the relatively primitive ichthyosaur *Cymbospondylus petrinus*, Merriam (1908) recognized three bones in the temporal region. An inner squamosal, an upper and outer supratemporal, and a lower quadrato-



jugal. On Watson's view we should have to believe that the quadratojugal of ichthyosaurs, in lizards, takes the place of Merriam's supratemporal. This seems unlikely.

Comparison of the occiput of *Cymbospondylus* with a disarticulated (and reassembled) skull of the pelycosaur *Diopeus leptcephalus* Cope would indicate that the element omitted in the phylogeny of the ichthyosaurs was the supratemporal. The remaining elements on this view would be a dorsal and inner tabulare, an upper, outer squamosal, and a lower quadratojugal. This returns to Williston's interpretation of the parapsid evolution and agrees with his "*Aræoscelis* theory" as to the origin of the lizard temporal elements.

Professor Gregory formerly favored the interpretation that Watson (1914) gives of the inner bone regarding it as squamosal. But he was inclined to doubt the advisability of calling the outer element quadratojugal and preferred to leave the outer element in lizards unnamed as an "X bone" (cf. Schmidt, K. P., 1919, Fig. 10).<sup>1</sup> Siebenrock has called it the paraquadrate. The views and synonymies of other investigators have been given by Baur, Thyng (1906), von Huene (1910b), Broom (1913), Watson, Methuen and Hewitt (1915), and Versluys (1919).<sup>2</sup>

Cope (1895a) and Williston consider the inner element in lizards as the one present in snakes. This would seem probable also from the facts outlined below regarding degeneration of the outer element in *Heloderma*. Both elements appear to be absent in the Uropeltidæ (Williston, MS., cf. Boulenger, 'Cat. Snakes,' I, p. 138).

Baur (1896) regarded the upper element in *Sphenodon* as the united squamosal (=tabulare) and prosquamosal (=squamosal). The topography and relationships of the single element present in *Sphenodon* would support this view. There is, however, not the slightest embryological ground for it at present. The results of Howes and Swinnerton (1903) and of Shauinsland (1903) show that the "squamosal" arises as a unit and that the flattened hook-shaped projection adjoining the end of the paroccipital process seems never to be separate from it. I am not sure that the ontogeny can give us a decisive answer to this question since even such recently united bones as the paired prevomers and the postfrontals and postorbitals are fused in the embryo of *Lygosoma* (cf. Siebenrock, 1892 and Pearson, 1921).

The shape and position of the two temporal bones are constant enough in lizards to enable us to be fairly certain of their identity in the

<sup>1</sup>After reviewing the subject and suggesting many points Professor Gregory now adopts the present view.

<sup>2</sup>Thyng, Versluys, and von Huene all regard the outer lacertilian element as the true mammalian squamosal.



group. I follow Williston and Broom in designating the inner as the tabulare (cf. Figs. 103, 106–109, and Text-Fig. C), reserving the name squamosal for the main posterior element of the supra-temporal arch.

The identification of the tabulare in geckos and in *Anniella* might be questioned because, with absence of the supra-temporal arch, there remains only a single element in place of the two (squamosal and tabulare) found in all lizards where skull arches persist. Which of these two bones the one in geckos represents is a difficulty that can be partly surmounted by examination of the analogous case in *Heloderma*. In this form, as in geckos, the supra-temporal bar is absent, but a small triangular rudiment of the squamosal remains alongside a large tabulare in normal position. The squamosal has been reduced to less than half the size of the tabulare, reversing the usual situation, and the tabulare remains apparently unchanged despite the reduction of the temporal arch. It would seem that in geckos also a reduction of the squamosal must have accompanied the reduction of the arches and that the bone remaining is the tabulare (cf. Fig. C) as its relations with the large (internal-posterior) head of the quadrate also would indicate (cf. Baur, 1889). There might still remain the question as to whether there actually has been a reduction and elimination of the supra-temporal arch in geckos or whether the conditions seen are a result of overgrowth of the parietal and fusion of that bone with the arch, thus eliminating the supra-temporal arcade. This is apparently what is about to occur in *Xantusia*, where both squamosal and tabulare are still present. If the outer element, squamosal, were to disappear in *Xantusia*, we should have exactly the conditions obtaining in geckos. But should the tabulare in *Xantusia* disappear, gekkonid conditions could not exist without great corresponding reduction and shifting of the squamosal.

The known distribution of the tabulare in lizards is as follows:—

Gekkota: Present in †*Ardeosaurus* (Fig. C), in *Pachydactylus*, *Hemidactylus*, *Gehyra*, *Tarentola*, *Sphærodactylus*, *Coleonyx*, *Uroplates* (cf. Siebenrock, 1893), and probably in most, if not all, other geckos as a small element.

Iguania: Very small in *Ctenosaura* and *Sauromalus*; present in *Iguana* (Beddard, 1905a) and *Conolophus* (Baur, 1896); a mere nodule in two species of *Anolis*; partly fused with squamosal in *Crotaphytus c. baileyi*; partly fused with parietal in *Calotes versicolor*; large in *Uromastix* (Beddard, 1905a) but concealed beneath the parietal process of the squamosal. According to Siebenrock (1895b) *Moloch* is the only agamid in which the element is lacking.



Rhaptoglossa: Present in *Chamæleon* as small element extending posteriorly inside the backwardly prolonged base of the squamosal; reduced to a vestige in *Brookesia* (cf. Siebenrock, 1893a, Pl. 1, fig. 4, s.t.); absent in *Rhampholeon* (Methuen and Hewitt, 1915).

Scincomorpha: Small in *Tiliqua* and *Egernia*; questionably present in *Acontias* (Gervais, 1853); present in *Voeltzkowia* (Rabanus, 1906–1915), in *Lygosoma*, *Mabuya*, *Eumeces*, and *Chalcides* (Siebenrock, 1892); a slender element in *Lacerta* and *Gerrhosaurus* (2 species); large in *Tejús* (cf. Hoffman, 1890) and *Tupinambis*; questionably present in some amphisbænians, cf. *Lepidosternon* (Gervais, 1853), *Amphisbæna* (= *Blanus cinerea*, Bedriaga 1884); absent in *Agamodon* (Peters, 1882) and in *Amphisbæna alba* (Williston, 1918, Fig. 4A).

Anguimorpha: Large in *Gerrhonotus* (Siebenrock, 1892); short and broad in *Ophisaurus*; large in *Anniella*; large, trihedral, and pointed in *Heloderma horridum* and in the †Glyptosauridæ; large in *Varanus* and †*Mosasaurus* (Cope, 1895a), †*Clidastes*, and †*Platycarpus* (=squamosal of Zittel); apparently fused with squamosal in *Zonurus*.

The os tabulare is regarded as a primitive saurian element which undergoes reduction and obliteration in a few of the higher Iguania and Diploglossa and in some of the extreme, burrowing amphisbænians.

## 5.—DEGENERATION OF EXTREMITIES AND GIRDLES

Reduction of feet, limbs, and girdles seems to be a fashionable course of devolution among autarchoglossine lizards. This process has occurred independently in many diverse groups, and seems to be rapidly going on at present among otherwise normal genera and species of scincs in widely separated parts of the world. Its investigation has naturally attracted a large number of students whose work has chiefly involved the examination of the morphological variations in limb structure.

On the morphological side, Fürbringer's summary (1869), of the osteological and myological structure of the limbs of some fifty-eight snake-like genera, is the most important contribution available. Cope (1892b), Fürbringer (1900), and Max Müller (1900) have investigated the reduction of the girdles in a number of forms, the former adding taxonomic views which differ generically from the system adopted by Boulenger. Cope following Gray (1845) regards as generic within the Scincidæ each grade of limb and foot reduction "so long as the characters are constant," admitting, however, the primary divisions of Boulenger. Boulenger's system seems the more natural and is widely adopted.



There is no case of the acquisition of complete limbs from a limbless or partly limbless progenitor in the whole of vertebrate history. This is a reasonably certain corollary of Dollo's law. We must proceed on the assumption at least that all limbless or partially limbed lizards have had fully limbed ancestors among their own kind, that in cases where a so-called degradational series exists such a series at least illustrates the probable stages of descent, and that in the cases where such a series is found within a single species the evolution of the end-stage must have been comparatively rapid admitting that the life-term of such a species is relatively short.<sup>1</sup>

We may fairly assume that total loss of limbs and girdles is entirely secondary—this is all the more certain since such conditions occur in reptiles only among the more advanced Ophidia. Total loss of the shoulder girdle among lizards is said to occur among the following forms:—

Scincoidea—Anelytropsidæ: *Anelytropsis papillosus*, Cope (1892b, p. 237).

Amphisbænoidea—*Anopsibæna kingii* Smalian, (1885), *Amphisbæna occidentalis*, Cope (*loc. cit.*, p. 241); *Rhineura floridana*, idem; *Cephalopeltis scutigera*, Müller (1900, p. 34); *Lepidosternon sphenorhynchum*, Peters (cited, in Müller, 1900); cf. also Fürbringer (1900, p. 261).

It has frequently been stated that *Anniella* has no trace of a shoulder girdle (cf. Cope, 1892a; Baur, 1894; Fürbringer, 1900, and Coe and Kunkel, 1906). A small cartilaginous element is present, however, in connection with several sets of muscles (cf. Figs. 70–72) and this element, if it represents a further evolution of the stages seen in *Ophisaurus* and *Anguis*, *Pygopus*, etc., must be the clavicle. In anguimorphs, the clavicle is not reduced as rapidly as the scapulo-coraco-sternoid complex; and in *Ophisaurus* (Müller, 1900, Fig. 4) the clavicle is partly cartilaginous. The muscles bear out the view that the element is the clavicle but it is possible, of course, that shiftings of insertion have occurred during degeneration.

Lönnberg (1916, Fig. 6) has given an interesting skiogram of the Siamese scinc *Isopachys gyldenstolpei*, and finds a rudimentary pelvis but no shoulder girdle. I am inclined to think that a small cartilaginous, splint-like shoulder girdle would not, if present, be shown in his picture for two reasons. (1) The direction in which the photo was taken (dorsal view) would show a lateral element only as a small dot. (2) Even

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<sup>1</sup>Born (1883) finds external, rudimentary forelimbs present in young embryos of *Anguis fragilis*, a genus totally limbless in the adult stage.



the presumably heavy parasternum, developed in all known subterranean scincs, appears only very faintly in the photo.

Boulenger (1887, 1912) has included as one of the family characters of the Dibamidæ, "no rudiments of the sternal apparatus." In a specimen at hand (A. M. N. H. No. 1264, ♀) of *Dibamus novæguineæ* there are present small bones connected with the most anterior parasternal chevron (which doubtless represents the sternum, cf. p. 390). These bones lie deep within the anterior fibers of the Obliquus externus profundus and are connected to this muscle by special slips (Fig. 75). There is also a serratus muscle running from the elements in question to the first thoracic rib. This relation, together with the similarity in appearance to *Feylinia*, which is not quite so far advanced (cf. Fig. 73), makes it seem that the rudiments present in *Dibamus* are the scapulo-coracoids.

When looking over such illustrations as those of Fürbringer (1900, Pl. XIII), Müller (1900), Rabanus (1906–1915), and Figs. 68, 73 and 75 of the present paper, in comparison with embryonic conditions as figured by Goette (1877) and Bogoljubsky (1914), one cannot fail to be struck by the marked resemblances of the extreme degenerative series to the early embryonic stages in such elements as the sternum and scapulo-coracoid. In *Blanus strauchii* for example (Fürbringer, Fig. 104), the sternal remnants are in the shape of two small cartilaginous discs quite separate on either side of the mid-line (cf. Bogoljubsky, 1914, Fig. 8). The united scapulo-coracoids are largely cartilaginous and quite widely separated medially. The interclavicle appears last in embryology and disappears first. The clavicle is the next in turn each way in scincomorphs. The sternum disappears before the scapulo-coracoids and appears later in the embryo; before final reduction it takes on the form of a parasternal chevron and at the final end-stages may resemble such fragments as are seen in the embryology of the salamanders (cf. Goette, 1877, Fig. 57).

Krieg (1919) after study of the shoulder girdle in seventy to eighty cleared specimens of *Lacerta serpa* and normal *Chalcides*, in comparison with degenerate *Chalcides tridactylus* and *Anguis fragilis*, decides that the intensity of variation in the bony elements is twice as great in *Anguis* as in the normal forms and that asymmetry develops frequently in the degenerates and rarely in the fully limbed genera. He regards extreme variation and asymmetry as symptoms of degeneration.

So far as known, vestiges, at least, of a pelvis, are always present in lizards.



Cope (1892*b*) has given results to show divergent tendencies of degeneration in different families:—

(1) Anterior limbs have disappeared more generally than the posterior in the Diploglossa and Pygopodidæ.

(2) The limbs incline to degenerate and disappear more nearly *pari passu* in the Scincoidea. (Anterior limbs persist in *Voeltzkowia* and posterior limbs are larger in *Neoseps*.)

(3) The anterior limbs have a tendency to persist longer in the Teiidæ and Amphisbænidæ (cf. Figs. 68 and 74).

Fürbringer's results (1869) show that there is no causal connection between the degeneration of a limb bone and the degeneration of the muscles inserting upon it. The muscle may lose its attachment and cease to function or be entirely reduced before the bone has disappeared, or the muscle may remain after the bone disappears. In degenerating limbs, the muscles, however, keep quite closely their original relations till the very last and usually disappear with the bone to which they are functionally attached.

It is apparent that few if any clues as to how or why special conditions have been brought about can be obtained from morphological study of degenerating parts. It seems that we should attempt to gather new facts from a comparative study of the special development of the trunk musculature to serve the needs of the changing habitus and habitat of the animal. The basis for such a work may be found in Smalian's classic '*Anatomie der Amphisbæniden*' (1885).

It is, of course, possible to arrange degradational series of living forms showing gradual degeneration of limbs, one toe at a time. Whether such a series illustrates the actual course of devolution does not concern us here. It is useful to know that full degeneration has taken place only in the most advanced types of burrowing lizards whose extraordinary development of body musculature, skull modifications, closure of ear, shortening of tail and loss of caudal chevrons, degeneration of lungs on one side, and loss of functional eyes, eyelids, sclerotic plates and osteoderms show in the most obvious way an extreme degree of specialization in connection with permanent subterranean life habits.

Such modifications in habitus have often obscured the heritage to such an extent that determination of original relationship becomes difficult. Even now we can but hint at the ancestry of the pygopodids and amphisbænids by emphasis of such conservative characters as tongue structure, form of vertebræ, pattern of throat musculature, and hemipenial texture.



High degree of convergence in habitus has frequently occasioned lumping of subterranean forms apparently of widely different ancestry. Most painstaking search for paleotelic characters will be necessary to correct this.

#### 6.—THE LUNGS

In limbed and in some limbless Squamata the lungs are developed equally on both sides. Butler (1895) has investigated the lungs in no less than fifty-nine species of snakes, belonging to nine different families, and in twenty-one species of lizards, including the following examples:—

Scincidæ: *Acontias meleagris*, *Acontias monodactylus*, *Scelotes bipes*.

Teiidæ: *Ophiognomon abendrothii*.

Amphisbænidæ: twelve species.

Pygopodidæ: *Pygopus lepidopus*, *Lialis burtoni*.

Anguidæ: *Anguis fragilis*, *Ophisaurus apus*, *Ophisaurus ventralis*.

Coe in Coe and Kunkel (1906) has studied the lungs of the anguioid *Anniella pulchra* and Bedriaga (1884) has examined certain typhlopine, rhinophine and calamarine serpents. Both Butler and Coe have checked the earlier work of Cope (1894 and 1900) and the results obtained show that in all forms except the Amphisbænidæ the left lung is the one to be reduced. In the Amphisbænidæ alone is the right lung reduced or absent. This would surely indicate that the Amphisbænidæ are not directly related to any known existing forms of limbless Squamata.

Milani (1894) distinguishes four degrees of differentiation of the lung structure in lizards. In the first or "Sphenodon-type," found in certain scincs and teiids, the lungs are simple alveolar-walled sacs without septa and differing from the Amphibia only in the specialization of the trachea. In the "Lacerta-type" found in *Gekko verticillatus*, *G. vittatus*, *Tarentola mauritanica*, *T. annularis*, *Gymnodactylus platurus*, *Thecadactylus rapicauda*, *Hemidactylus turcicus*, *Calotes jubatus*, *Tiliqua*, *Lacerta ocellata*, *L. agilis*, *L. viridis*, and *Zonurus giganteus* there are a number of septa dividing a portion of the lungs into small internal chambers. This type is developed from the first by enlargement of some of the alveolar walls and is not essentially different from the first. The "Iguana-type" is still more highly specialized by marked extension and enlargement of the less numerous septa. This type is found in a number of iguanids and agamids. The lungs of *Heloderma* and *Phrynosoma* approach but do not attain the typical development of this type. The "Varanus-type" is by far the most highly modified of all with long internal bronchi and a spongy internal reticular network much as in mammals. The "avian" lungs of *Uroplates* and *Polychrus* have the



finger-like processes characteristic of some chameleons (cf. Methuen and Hewitt, 1915). Internal septa are developed as in the "Iguana-type." In *Amphisbæna* and *Anguis* the internal structure is simple.

#### 7.—FUSION OF MEDIAN SKULL ELEMENTS

In *Aræoscelis* (Williston, 1914, Fig. 3*B*) all the median skull elements are paired. This condition also obtains in a few geckos, *Phyllurus* (cf. Cope, 1892*a*).

The premaxillaries are paired only in some Gekkonidæ and in the Scincidæ.

The nasals are paired in all forms except the Uroplatidæ; the chamæleontid, *Brookesia*; the Varanidæ; Aigialosauridæ; Mosasauridæ (?)<sup>1</sup>; and Feyliniidæ.

The frontals are separate in the Ardeosauridæ, in some Gekkonidæ, some Scincidæ, in the Feyliniidæ, Gerrhosauridæ, some Lacertidæ, the Amphisbænidæ, Varanidæ, Dolichosauridæ, Helodermatidæ, some Anguidæ, and in the Anniellidæ.

The parietals are paired only in some Gekkonidæ, and in the Uroplatidæ and Xantusiidæ. There is a partial suture, according to von Huene (1910*b*), in *Tylosaurus dyspelor*. Some Glyptosauridæ appear to have a suture.

The primitive nature of unfused paired skull elements is usually acceded to in accordance with the fossil evidence. Méhely inclines to the view, however, that embryonic or post-embryonic paired conditions may prevail in descendants of a series of ancestors with fused elements, thus upsetting any scheme based on progressive fusion and non-disjunction of once fused elements (cf. p. 404). Whatever may happen, it is certain that the point of least fusion occurs just where we might expect it should *a priori*—that is among the geckos, and that end-branches of the phylogeny have the greatest extent of fusion of skull elements.

The chameleons, iguanids and agamids, helodermatids, varanids and teiids, and certain of the burrowing degenerates have the greatest amount of fusion. The amphisbænids are relatively primitive in this as in vertebral characters.

#### 8.—THE PREVOMER

Broom (1914) considers the mammalian vomer as represented in reptiles by the parasphenoid and thinks that the so-called lacertilian "vomeres" are homologous with the "dumb-bell bone" of *Ornitho-*

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<sup>1</sup>Von Huene (1910*b*) states that isolated, small nasals are present in *Tylosaurus*.



*rhynchus* and with a similar bone in certain bats. He has named the lizard "vomer" the prevomer, a designation lately accepted by Williston and by Watson. Whether or not the mammalian vomer represents the parasphenoid does not discount the value of Broom's demonstration of fundamental difference between the so-called "vomeres" of reptiles and the true mammalian vomer. Consequently it seems advisable to adopt Broom's terminology.

Cope (1892a) states that the "vomeres" of lizards are separate in all forms except *Chamæleon*. This is incorrect. The prevomers are completely fused in the scincs *Lygosoma*, *Chalcides*, and *Ablepharus*, and partially so in many other scincs, gerrhosaurids, lacertids, and anguioids (Siebenrock, 1892, 1894). They are quite separate in the primitive scincs *Trachysaurus* and *Tiliqua*, in *Tupinambis*, the *Amphisbænidae*, *Zonurus*, and *Varanus*. They are rarely fused in iguanids (*Crotaphytus c. baileyi*) and are not known to be fused in other groups with the exception of the *Agamidæ* (cf. Siebenrock, 1895b) and *Chamæleontidæ* where they are generally united. Boulenger (1887) states that they are single in the latter group. Cope (1900, p. 209) refutes this and at this date states the "vomer" to be paired in chameleons. Siebenrock (1893a) after careful examination of *Chamæleon vulgaris* determined the "vomer" to be "entschieden unpaarig." Cuvier and Brühl (1888) regard it as paired, Blanchard, Parker (1881) and Born as unpaired. Parker's figures show that the "vomer" in the specimens he had of *Chamæleon vulgaris* and *C. pumilus* was partly divided. A specimen of *Chamæleon* in the Department of Comparative Anatomy of the American Museum has traces of a median suture in the prevomer. Another unidentified skull has no suture. Specimens at hand of *Chamæleon vulgaris* and *C. gracilis* have a single median element occupying the usual position of the lacertilian "vomer" and separated from the premaxilla and palatines by definite sutures.

Lying on either side of the "vomer" in the carefully prepared skull of *Chamæleon vulgaris* are delicate triangular elements underlying Jacobson's organ. These lateral bones are apparently broken away in the rough skeleton of *C. gracilis* which shows, after preparation, an unpaired median prevomer. Possibly these lateral elements represent the "maxillo-palatines" of Cope, but this does not seem very likely. They appear to be cartilage bones identifiable with the cornu trabeculæ of Parker (1881).

Siebenrock (1893a) considers the "vomer" to be absent in *Brookesia* and from his figures I should regard it as fused with the inferior spine of



the premaxillary. Methuen and Hewitt (1915) record the absence of the "vomer" in *Brookesia* and *Rhampholeon*.

There is little question but that the prevomer of the chameleons represents the fused "vomeres" of other lizards and was originally a double element. It seems also that the differences in descriptions of the chameleon prevomer are due in no small part to actual variations in different species and individuals.

### 9.—THE HEMIPENES

The external form of the copulatory organs or hemipenes of the Sauria would appear from the recorded investigations of Cope (1896b) to have an important bearing on the phylogeny and classification. No illustrations for the lizards accompanied the terminology of Cope and it might be helpful to compare his descriptions with figures given by Gray (1870, *Varanus*), Leydig (1872, Pl. ix, fig. 118, *Anguis*; figs. 125 and 126, *Lacerta agilis*), Fleischmann (1902, Pl. viii, figs. 1 and 7, *Platy-dactylus guttatus*; figs. 2 and 6, *Anguis*), and Coe and Kunkel (1906, Pl. XLIV, figs. 30–32, *Anniella*).

Cope's view was that "the higher Sauria have the parts modified as in the serpents by the presence of calyculi. Such are characteristic of the Rhiptoglossa and Pachyglossa (= Iguania). The Nyctisaura (= Gekkota) possess the same feature. The Diploglossa, Helodermatoidea, and Thecaglossa (= Varanoidea) have the organ flounced, the flounces often pocketed or repand on the margin. In the Leptoglossa (= Scincomorpha) we have laminæ only; in the Teiidae mostly transverse and in the Scincidae mostly longitudinal. In various genera terminal papillæ are present. The organ may be simple or bifurcate or merely bilobate." In the Zonuridae there are still traces of calyculi. In the Xantusiidae and Xenosauridae, the form is peculiar. All the groups included in my Ascalabota have calyculate hemipenes; all those in the Autarchoglossa, with the exceptions noted, have the organ flounced or laminate. In the Serpentes, calyculi, spines and flounces are present in varying degree. The spinous character is a decided similarity to the Anguimorpha.

Fleischmann has shown that the hemipenes originate in both snakes and lizards in the same way from the ectoderm of the lateral corners of the cloacal lips.

Cope's statement that the organs are calyculate in the "higher Sauria" does not exactly fit his phylogenetic scheme (1900), where he considers the calyculate forms, Pachyglossa (= Iguania), as ancestral. He is again forced to regard the close resemblances of serpents to the



anguimorphine lizards as due to convergence (p. 196) because of his preconceived idea of separation between the "Pythonomorph" and saurian lines (p. 180). I cannot regard the Serpentes as anything but highly modified anguimorphine lizards near the platynotid stock. The detailed hemipenial resemblances in addition to similar characters in the vertebræ, skull, teeth, and tongue in varanids and ophidians,—the similar reductions of the body segments in certain autarchoglossids and in the serpents, and the details of the throat musculature would seem to preclude any possibility of convergence, especially since the many characters separating the lizards and true snakes are not much beyond the range of differences found among certain snake-like lizards. Among such characters may be included: absence of temporal arches, jugals, squamosals, lacrymals, postoptics, and epipterygoids; and reduction of bones in the lower jaw.

#### 10.—THE NUMBER OF CERVICAL RIBS

Lizards may be said to have, typically, six or eight cervical vertebræ, depending on the way they are counted. I should consider all vertebræ whose ribs ever attain a connection with the sternum, to be dorsal. Since the elongate rib of the so-called eighth "cervical" sometimes has a sternal connection (Fig. 68) and since the seventh "cervical" is so obviously a pair to it, there may be some advantage in considering six the typical number. Cope and Siebenrock regard the number as eight.

All lizards as far as known have six cervicals except *Varanus* and the Mosasauroids (Platynota) which have seven, the allied Dolichosaurs which have thirteen, and the Chamæleontidæ which have only three. The number in many limbless forms, of course, is not ascertainable. These forms usually have three anterior cervicals without ribs, as in most lizards, and it may be well to consider the number in all such forms as six. This will provide a comparative basis for rib-counts.

In the following table those genera followed by a letter (C) are given on the authority of Cope (1892*a*). It may be noted that families and genera (Gekkonidæ, Scincidæ), considered primitive on other grounds, have greater numbers of cervical ribs than do groups of less paleotelic weight (Agamidæ, Chamæleontidæ).

Four cervical ribs:

Gekkonidæ: *Coleonyx*, *Phyllodactylus* (2 species), *Pachydactylus*.

Scincidæ: *Egernia*, *Trachysaurus*, *Tiliqua*.

Three cervical ribs:

Gekkonidæ: *Gehyra*, *Phelsuma*, *Thecadactylus*, *Gonatodes*, *Lathrogecko*, *Lepidoblepharis*, *Sphærodactylus*.



Iguania: *Uromastix*, *Sceloporus* (C) 2 species, *Phrynosoma*, *Crotaphytus* (2 species), *Holbrookia*.

Scincomorpha: *Xantusia*, twenty species of Scincidæ according to Siebenrock (1895a), *Gerrhosaurus*, *Lacerta*, *Cnemidophorus* (C), *Tupinambis*, *Bachia*, *Amphisbæna*, *Rhineura* (C).

Anguimorpha: *Gerrhonotus* (C), *Ophisaurus*, *Anguis*, *Heloderma*, *Zonurus*.

Two cervical ribs:

Iguania: *Calotes versicolor*, twenty-nine species of Agamidæ according to Siebenrock (1895b), *Norops*, *Xiphocercus*, *Anolis*, *Iguana*, *Sauromalus*, *Dipsosaurus* (C), *Callisaurus*, *Chalarodon*.

One cervical rib: *Draco formosus*, (?) *Chamæleon gracilis*.

No cervical ribs: *Chamæleon vulgaris*.

The only lizards I have noted which bear ribs on the third (first post-axial) vertebra are the primitive geckos, *Coleonyx*, *Phyllodactylus*, and *Pachydactylus*; the primitive Australian scincs, *Egernia*, *Trachysaurus* (cf. Werber, 1895) and *Tiliqua*; and a species of *Chamæleon*. The latter case is remarkable but not strictly comparable with the others and probably not indicative of primitiveness since it may be due to ex-  
calation of the more anterior vertebræ.

Professor Osborn (1899, p. 179) states that the third cervical of *Tylosaurus* bears "a small rib, which is not preserved." The appearance of the cervical diapophyses in varanoids and other lizards, however, may be deceptive and the evidence should be conclusive before allowing the mosasaurs an extraordinary number of ribs. I have found only two cervical ribs in our skeletons of *Varanus*.

#### 11.—THE POSTFRONTAL AND POSTORBITAL

We are indebted to Siebenrock for accurate observations upon the osteology of lizards. Data from his papers are credited by the letter (S).

Some confusion prevails concerning the disposition of the postfrontal and postorbital in lizards. By tracing through a series of forms in the Scincidæ (*Lygosoma*) where fusion sometimes occurs, it is found (S., 1895b) that in this group the postorbital grows smaller and is finally absorbed by the postfrontal. On the other hand, if Beddard (1905a) is correct in his recognition of an anterior postfrontal in *Uromastix*, the large element present in the Agamidæ is the postorbital. An examination of the analogous case in *Iguana* and *Sauromalus* shows that here also the larger element is the postorbital, as its relations with the squamosal would further indicate.



In existing Gekkota the single element present, as shown by its relations to the frontal, the parietal, and the postorbital ligament, is the postfrontal.

We have then the following relations:—

Gekkota: postfrontal only. In *Ardeosaurus* the single bone present (Fig. C, *Po*) may represent the fused postfrontal and postorbital.

Iguania: postorbital large; postfrontal small (*Iguana*, *Sauromalus*, *Uta thalassina*, *Uromastix spinipes*) or absent (*Crotaphytus collaris* and most Agamidæ, S, 1895b).

Rhaptoglossa: it is impossible to say what the single bone present represents.

Xantusiidæ: anterior postfrontal and posterior postorbital both large and separate in *Lepidophyma* (Duméril and Bibron, 1870); fused into a single broad postfronto-orbital (*Xantusia vigilis*, *X. riversiana*).

Scincidæ: median postfrontal large, lateral postorbital moderate (*Chalcides simonyi*, S, 1892); postfrontal large, postorbital small (*Mabuya multifasciata*, *Ablepharus*, *Lygosoma quoyi*, S, 1892); postfrontal large, postorbital absent (most Scincidæ, including many species of *Lygosoma*).

Gerrhosauridæ: a small anterior postfrontal and a large posterior postorbital exluded from the orbit, (S, 1892).

Lacertidæ: postfrontal and postorbital of about equal size and separated by a longitudinal suture (*Lacerta dugesii*, *L. ocellata*, *L. viridis*, *L. agilis*, *L. muralis*, *L. oxycephala*, *L. mosorensis*, *Algiroides*, *Acanthodactylus*, *Ophiops*, S, 1894) or a single, fused postfronto-orbital (*Lacerta simonyi*, *L. galloti*, *L. atlantica*, *L. vivipara*, *Tachydromus*, *Psammodromus*, *Eremias*, S, 1894).

Teiidæ: postfrontal a small anterior element, postorbital long, slender, and extending far posteriorly along the squamosal (*Tupinambis*); the elements are fused in *Cnemidophorus* (Cope, 1892a).

Amphisbænidæ: postorbital only, in *Amphisbæna alba* (Williston, 1918); both elements absent in *Agamodon* (Peters, 1882), in *Blanus cinereus* (Bedriaga, 1884), and in *Amphisbæna fuliginosa*, *Lepidosternon* and *Trogonophis wiegmanni* (Gervais, 1853).

Anguimorpha: postfrontal and postorbital separate and of nearly equal size (Anguidæ, Glyptosauridæ and Aigialosauridæ, Nopcsa, 1903) (cf. Figs. 103, 106–108); fused (Varanidæ and Mosasauridæ, Baur, 1892); separate but postfrontal much smaller (Zonuridæ); postfrontal present and in contact with prefrontal, no postorbital (*Heloderma*, *Lialis*); neither postfrontal nor postorbital (*Ophioseps*, Jansen, 1901).



In the Xantusiidæ, Gerrhosauridæ, and the Lacertidæ, the supratemporal fenestra is entirely closed by the backward growth of the postorbitals. In the Scincidæ (*Mabuya*), this occurs by backward prolongation of the postfrontals.

By the relations and variations of these elements we may distinguish the following groups of lizards: Gekkota, Iguania, Rhiptoglossa, Scincidæ, Xantusiidæ+Lacertidæ+Gerrhosauridæ, Varanidæ+Mosauridæ, Anguidæ+Glyptosauridæ, *Heloderma*+*Lialis*.

## 12.—THE LACRYMAL

The lacrymal in lizards is small, when present, and surrounds or lies externally to the lacrymal canal at the antero-inferior margin of the orbit (cf. Gregory, 1913, 1920, p. 131).

The primitive state of the lacrymal in parapsids is probably that illustrated in *Aræoscelis* (Williston, 1914, p. 135, and Fig. 3A), where it is already small but still apparent externally as a short bar between the prefrontal and jugal. This is its position in the primitive orbital ring of the stegocephalians and cotylosaurs (Gregory, 1920, Figs. 12, 14, 18, 33, 34, etc.). In some lizards (cf. Teiidæ and some Iguanidæ) a condition similar to that in *Aræoscelis* is maintained; in others (Varanidæ and Helodermatidæ) there is a shortening and thickening of the bone. In the Gekkonidæ the lacrymal is crowded within the orbit and lost to view externally. I have not been able to discover the element in *Xantusia vigilis* (it is slightly fused with the prefrontal in *X. riversiana*), nor in the Scincidæ, Feyliniidæ, Gerrhosauridæ, Lacertidæ, Amphisbænidæ, and Zonuridæ. Cope (1892a) states that in the Scincidæ it has fused with the prefrontal and this may have occurred among certain other groups (cf. *Lacerta*) where the lacrymal tubercle seems to be present on the prefrontal.

In a skull of *Chamæleon gracilis* at hand, the lacrymal is certainly present as a long, thin, external element. In the related genus *Brookesia* it appears from Siebenrock's figures (1893a) to be absent.

In the Agamidæ it is often small and is absent (Siebenrock, 1895b) in: *Draco*, *Sitana*, *Lyriocephalus*, *Calotes versicolor*, *C. mystaceus*, *Agama sanguinolenta*, *A. pallida*, *A. hispida*, *Phrynocephalus*, *Amphibolurus* and *Uromastix*.

What little we know, accordingly, of the distribution of the lacrymal appears not specially significant. Its characteristic shape has been lost in *Heloderma* and *Varanus* and obscured in the geckos and in those families where fusion has occurred. Small elements such as the lacrymal and intermedium are not of great importance in the phylogeny because of their sporadic disappearance and fusion.



## 13.—THE MANDIBULAR TEETH

There has been no uniformity of opinion as to what kind of tooth-insertion is oldest in the Sauria. *Aræoscelis* is described as having thecodont or proto-thecodont teeth, subconical (solid?), nearly homodont, and simple—without accessory cusps (Williston, 1914, p. 118–119). In the Eocene of North America we find both acrodont and pleurodont types of dentition. In the Phosphates of Quercy (Eocene-Oligocene), both types are present. Boulenger, basing his views doubtless on the conditions in the Rhynchocephalia, considers acrodonty as primordial in lizards. Cope regards the acrodont and pleurodont series of parallel value and expresses the view (1900, p. 206) that the Pachyglossa (Iguanidæ and Agamidæ) are “probably ancestral to the other superfamilies. The dentition of the Agamidæ is quite identical with that of many of the Rhynchocephalia, and with that of the chameleons as well. It is a modification of the primitive rhizodont dentition which prevailed during the Permian.”

The teeth of the Jurassic Euposauridæ are not certainly pleurodont (cf. p. 319). Those of *Chamops* from the Laramie Cretaceous are not typically so (cf. p. 309). It would seem from what we know of the record, that thecodonty has preceded both pleurodonty and acrodonty in the saurian line. It also appears from comparative evidence and from the embryology that thecodonty or pleurodonty has in every case preceded acrodonty. Siebenrock (1895*b*) shows that the developing tooth in *Agama* goes through a pleuro-thecodont stage. Carlsson's results (1896) are also interpreted in this way. It seems probable that the transitions such as seen in Teiidæ, Varanidæ, Helodermatidæ, and Amphisbænidæ are developing in the direction of acrodonty rather than pleurodonty. All the more so since in the subpleurodont, advanced, limbless scincs and anguids this would be most likely owing to undoubtedly recent development from pleurodont ancestors. Some forms of *Ophisaurus* (cf. *O. harti*, Boulenger, 1899*a*) have a subacrodont, pythonomorph dentition like that of *Anguis* (cf. Leydig, 1872). The typical dentition of *Ophisaurus* is subpleurodont. The dentition of the limbed anguids is pleurodont (cf. Figs. H, I).

If we regard the thecodont dentition of *Aræoscelis* as primitive we should consider the pleurodont condition as developed from it by breaking down of the lingual alveolar walls and lengthening of the tooth crown, which becomes a hollow, cylindrical shaft.

The highly acrodont teeth of the Agamidæ and Chamæleontidæ may have arisen directly from a thecodont type by atrophy and shorten-



ing of the base and coincident replacement of the alveolar cups by infilling of mandibular bone or, as seems less likely, by such modifications directly from pleurodontology as might be illustrated in many stages among various living forms.

We may, therefore, question the advisability of Cope's view of the primitive status of the agamids. It is among the Agamidæ that some of the most specialized types of lizards are developed. The relations of this family to the chameleons seem not distant and it can also be demonstrated that there is scarcely anything primitive in the structure of the chameleons. It is among the Agamidæ that the most heterodont types of Saurian dentition occur and this again would make it appear that the acrodont series cannot be considered primitive.

Another feature which marks the hyperacrodonty of *Sphenodon* and the Agamidæ and Chamæleontidæ as a highly specialized condition is the failure to develop replacement teeth in the adult. Harrison (1901) has shown that in *Sphenodon* there are no replacement teeth developed after the first five dentitions of the embryo. Röse (1893) finds that there is no succession or shedding even in the young of chameleons. He did not study the embryos. Carlsson (1896) discovers a succession in embryos of *Calotes* but mentions none beyond the embryonic stages. She does, however, state that the persistence of an enamel organ into late life is a resemblance to the pleurodont lizards not to be seen in *Chamæleon*. Woerdeman (1919), without knowledge of the results of Carlsson, and after study of snakes and many pleurodont lizards, found old embryos of *Calotes* to represent "das einzige Reptil gewesen we ich die Alternierung nicht auffinden konnte."

When the teeth become worn or broken away in the hyperacrodont lizards, enamel is sometimes deposited upon the edges of the mandibles (cf. *Uromastix* and *Sphenodon*) which then take on a masticatory beak-like function.

Succession occurs throughout life among pleurodont lizards. In the most highly developed types of pleurodontology such as occur among the Iguania and Scincomorpha, the teeth are hollow, thin-walled cylinders which receive the replacement teeth into their bases (cf. Leydig, 1872). Among the more solid toothed anguimorphs this occurs only in the Zonuridæ. Even in *Gerrhonotus* (Fig. H), which is quite typically pleurodont, the new teeth lie outside the old. There is evidence of similar replacement in the Eocene Glyptosauridæ (Fig. I). Among the subacrodont anguimorphs, the replacement is strictly alternate.



## 14.—THE PALATAL TEETH

Pterygoid teeth are present in many Iguanidæ, Scincidæ, Gerrhosauridæ, primitive Lacertidæ, Glyptosauridæ, Cretaceous Platynota, Anguidæ, and in some Teiidæ (cf. Boulenger, 1885–1887, and 1920; Cope, 1892*a*, Siebenrock, 1892). Genera of Iguanidæ with such teeth are given in Boulenger 1885: [*Crotaphytus*, 1 species with, 1 species without, *Sauromalus hispidus*], *Dipso-saurus*, *Ctenosaura*, *Brachylophus*, *Cyclura*, *Hoplocercus*, *Metopoceros*, *Iguana*, *Conolophus* (in young), *Amblyrhynchus*, *Phymaturus*, some *Uraniscodon*, *Tropidurus*, most *Leiocephalus*, *Saccodira*, *Liolæmus*, *Ctenoblepharis*, *Stenocercus roseiventris*, *Stenocercus cupreus*, *Hoplurus*, *Chalarodon*, *Pristidactylus*, *Liosaurus*, *Urostrophus*, most *Enyalius*, *Enyalioides*, *Ophryoessa*, *Basiliscus*, *Læmanctus*, *Corythophanes*, *Polychrus*, *Tropidodactylus*, most *Anolis*, *Xiphocercus*, *Chamæleolis*.

Among Scincomorpha having pterygoid teeth those listed by Siebenrock (1892 and 1894) are: *Mabuya multifasciata* (2 teeth), *Eumeces schneideri* 6, *Gerrhosaurus nigrolineatus* 5, *Zonosaurus* 6, *Algiroides* 2 to 3, *Tachydromus* 3 to 4, *Eremias* 5 to 6, *Lacerta muralis* 6 to 7, *L. oxycephala* 6 to 7, *L. atlantica* 6 to 8, *L. viridis* 8 to 10, *L. agilis* 10 to 12, *Psammodromus* 10 to 12, *L. galloti* 12 to 14, *L. simonyi* 13 to 16, *L. ocellata* 16 to 20,—genera with more than eight teeth having several rows.

Anguimorpha with pterygoid teeth are: the Aigialosauridæ, the Mosasauridæ, *Heloderma*, *Lanthanotus*, the Glyptosauridæ, *Gerrhonotus*, and *Ophisaurus*.

Hilgendorf (1885) figures prevomerine teeth in *Pseudopus pallasii* (= *Ophisaurus apus*) and notes that there are a greater number of such teeth present in his fine specimen of *Propseudopus fraasii* from the upper Miocene of Steinheim. Prevomerine teeth occur in a specimen of *Ophisaurus* at hand (2 to 3 on each side). *Ophisaurus*, having the most dentigerous palate of all living lizards, is the only recent genus known to have prevomerine teeth (cf. Brühl, 1875–1888). They are present in the Eocene diploglossids, the Glyptosauridæ.

The palate appears to be toothless in the Gekkonidæ, Uroplatidæ, Pygopodidæ, some Iguanidæ, the Agamidæ, Chamæleontidæ, Xantusiidæ, some Scincidæ (*Trachysaurus*, *Tiliqua*, and *Egernia*), the Anelytropsidæ and Dibamidæ, some Lacertidæ (*Ophiops*), some Teiidæ, the Amphisbænidæ, most Anguidæ (including some species of *Gerrhonotus*, all known *Diploglossus*, *Ophiodes*, and *Anguis*), the Annielliidæ, Xenosauridæ, and in the Zonuridæ.



The Iguanidæ without palatal teeth, according to Boulenger (1885) are: [*Crotaphytus c. baileyi*], *Callisaurus*, *Holbrookia*, *Phrynosoma*, *Uta*, *Sceloporus*, *Urocentron*, *Strobilurus*, some *Uraniscodon*, some *Leiocephalus*, *Helocephalus*, *Stenocercus marmoratus*, *S. torquatus*, *S. humeralis*, *S. varius*, *S. moestus*, *Scartiscus*, *Diplolæmus*, some *Anolis*, *Norops*.

I should consider the simple presence of teeth on the palate as paleotelic. Such teeth would seem to be ancestral owing to lack of development in secondary lines of descent, and prevalence of teeth in greater numbers in certain more ancient forms. One may not, however, regard the distribution of such teeth as of paleotelic significance owing to the likelihood of dropping out, development and migration of cutaneous tooth buds from one bone to another in the course of recent phylogeny.

#### 15.—THE INTERCLAVICLE

The classic view of Gegenbaur (1865), supported by the paleontological and to a considerable extent by modern embryological evidence, is that the clavicle and interclavicle are secondary "derm-bones" of later origin than the so-called primary shoulder girdle. Goette (1877) did not accept this theory believing that the clavicle in lizards arises as a part of the cartilaginous scapulo-coracoid anlage. Bogoljubsky (1914) reconciles the embryological history in lizards at least partially with Gegenbaur's conclusions, showing that the clavicle is not preformed in cartilage and develops for the most part independently and originally in close connection with the skin. The interclavicle develops from the median ends of the clavicular fundamentals as a paired structure (Goette and Bogoljubsky). According to the latter, it takes on very early in *Lacerta* the broadened rhomboid form comparable with the shape found in certain Permian amphibians, *Palæohatteria*, and some of the cotylosaurs.

We know nothing of the condition of the interclavicle in the ancestral Squamata. In *Proterosaurus* it is represented as in Fig. 76. It reaches its highest development among the stegocephalous Amphibia as a rhombic plate. It disappears rather early in mammalian history. It is not present in the birds. From its distribution we have reason to believe that reduction of various parts of the interclavicle is taking place in the Sauria. Such reductions seem to have occurred locally among the Gekkota, almost universally among the Iguania, and also in other groups.

In the Gekkonidæ, a subrhomboid plate-like form appears in some genera. Such a form obtains in the amphiœlous *Gehyra* and *Gonatodes*; and in the proœlous *Coleonyx*. In the apparently more advanced



*Lathrogecko*, and *Sphærodactylus* (cf. Noble, 1921) a sub-cruciform shape is attained; in *Phyllodactylus* as well. In *Paragonatodes* further reduction takes place and a splint-like longitudinal element remains. In *Uroplates* only a nodule occupies the position of the interclavicle.

Among the Iguanidæ most forms have a typically T-shaped or anchor-shaped element of possible derivation from the cruciform shape. In *Phrynosoma* (Fig. 45) this is reduced by elimination of the lower bar. In the Agamidæ (cf. Siebenrock, 1895*b*), great variation occurs. The two primitive genera *Liolepis* and *Uromastix* retain the cruciform shape. In *Phrynocephalus* this has been apparently transformed into an anchor. In *Draco*, *Sitana*, *Lyriocephalus*, *Gonocephalus*, *Acanthosaura*, *Calotes*, *Japalura*, *Charasia*, *Amphibolurus*, an arrowhead is found similar to that seen in *Xantusia* (Fig. 69). *Agama* has a small T-shaped element, *Moloch* a plate.

The interclavicle is considerably reduced in *Draco*, *Sitana*, *Lyriocephalus*, *Gonocephalus*, *Japalura*, *Charasia*, and in most species of *Agama* and *Phrynocephalus*. It is altogether absent in the Chamæleontidæ.

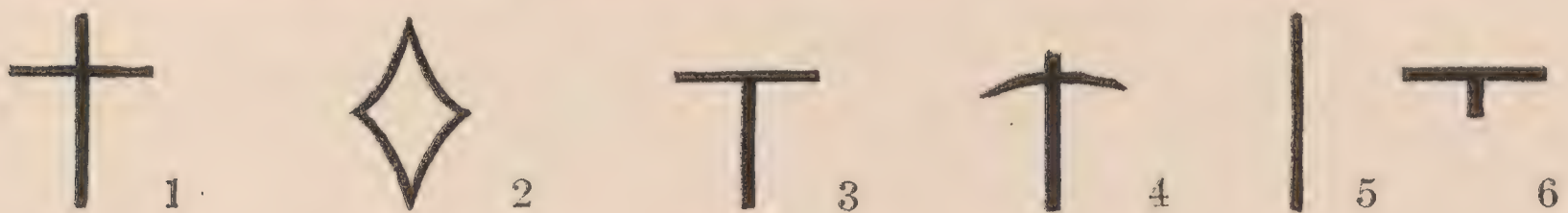


Fig. J. Various types of saurian interclavicles.

According to Boulenger, in the Xantusidæ alone among the limbed scincomorphs is a T-shaped form present. *Xantusia vigilis* and *X. riversiana*, however, have a cruciform shape (Fig. 69) characteristic of all fully limbed scincomorphs. In *Chalcides lineatus* this form is retained; in the limbless *Evesia* (*Acontias monodactylus*) only a longitudinal bar remains (Cope, 1892*b*, Fig. 9), this is the condition in the teiids *Ophiognomon* and *Bachia* (Fig. 68); in *Chirotes*, the only amphisbænian with limbs, there is no interclavicle.

Among the Anguimorpha, all the limbed Anguidæ and all the Zonuridæ have the cruciform shape. In the Helodermatidæ, the interclavicle is reduced to a thin, longitudinal rod, and in the Varanidæ, Aigialosauridæ and Xenosauridæ to an anchor-shaped element. The interclavicle appears to be absent in the Dolichosauridæ and in most of the Mosasauridæ. Among the limbless Anguidæ, *Ophisaurus ventralis* and "*Pseudopus pallasii*" retain a T-shaped form with the lower bar reduced. *Anguis fragilis* has but a variable nodule remaining, sometimes cruciform (cf. Krieg, 1919). In the embryo of *Anguis* the cruciform



shape persists (Goette, 1877). According to Cope (1892*b*), in *Ophiodes striatus* conditions are similar to *Ophisaurus pallasii* but with a broad separation between sternal plate and interclavicle; in "*Dopasia*" *gracilis* and in the Pygopodidæ, the interclavicle is wanting.

The interclavicle in Sauria is connected with certain muscles of the neck and shoulder (Figs. 63–67). The attachments of these muscles seem directly responsible for its cruciform shape in many groups (Fig. J1). This, it would appear, is a modification of a still more ancient condition (Fig. J2) retained by certain geckos. The action of the deltoid and pectoralis muscles would presumably account for the hollowing out of the four sides of the rhomb. The retention of the arms is due to the attachments by fascia of the extremely heavy sternohyoid and sternothyroid muscles serving the head. Reductions of the cruciform interclavicle to the forms indicated in Figs. J3, J4, J5, and J6 are all seen in various groups. And it seems likely that these further reductions have all been derived from a cruciform condition (cf. Fürbringer, 1900).

#### 16.—THE CLAVICLE

The clavicle as known in *Aræoscelis* (Williston, 1914, Pl. iv, fig. L) is expanded toward the mid-line and imperforate. Similar conditions are seen in the primitive Australian scinc, *Trachysaurus* (cf. Werber, 1865), where the expansion is carried to a higher development. In *Trachysaurus* and in the nearly related *Tiliqua* and *Egernia* more or less perforation sometimes occurs in the broadened end. Many of the geckos have broadly expanded perforate clavicles and whenever the clavicle is rod-shaped in the geckos it seems to bear trace of a former breadth and perforation (cf. Noble, 1921, Figs. 4 and 5).

These conditions among primitive groups lead me to believe that broadly expanded, non-perforate clavicles are ancestral among modern Sauria and that simple rounded clavicles have been shaped from these.

The origin of the peculiarly reflected portion of the Clavodeltoideus should be understood (Figs. 63–67) when examining the correlated morphological conditions. This muscle passes over the anterior edge of the clavicle from the dorsal side, arising on the ventral border of the bone in the broadly expanded autarchoglossid types. The perforation occurs under the belly of this muscle and may be concerned with the action of the muscle. Further development of the muscle, as in the case of the interclavicle, apparently means reduction of the clavicle, first to a hook-like form, then to a bar.



In *Uroplates* the clavicle is elongate and simple. In the Iguanidæ it is usually simple, but two known genera (*Basiliscus* and *Læmanctus*) have retained or regained a loop-shaped form (Boulenger, 1885). The Agamidæ have a simple and delicate bone which is hook-shaped in *Lyriocephalus* and broadened laterally in *Liolepis* and *Moloch* (cf. Siebenrock, 1895b). In the chameleons clavicles are absent or rudimentary in the adult but "fairly well developed" in the embryo (Broom, 1906).

In all limbed and many limbless Scincomorpha, the clavicle is dilatated and frequently perforate or hook-shaped. The latter form constitutes an apparent advance from the perforate condition occurring in the Teiidæ which rarely (*Tretioscincus* and *Scolecosaurus* Cope, 1892a) have simple clavicles. Goette (1877) finds in the embryo of *Cnemidophorus* a perforate clavicle which later develops a hook-shape typical of the Teiidæ. In the Scincidæ and Gerrhosauridæ, the element is unusually broad and generally perforate. In Lacertidæ, narrower and always perforate.

In the Anguimorpha, the clavicle is always simple (Fig. 81). It is absent only in certain mosasaurs and in the dolichosaurs.

Among the limbless Scincomorpha, the clavicles always disappear before the scapulo-coracoids (cf. Müller, 1900, Figs. 7, 8 and 9; Cope, 1892b, Pl. XIII, fig. 12). In the Anguimorpha the clavicle seems to persist after all the other elements have vanished (cf. Figs. 70–72 with Figs. 73 and 75). In final stages of reduction both scapulo-coracoid and CLAVICLE become cartilaginous but retain characteristic muscle connections. In many cases (Amphisbænidæ, *Acontias*, Anguidæ), the course of reduction can be followed through various stages in related forms (cf. Müller and Cope, *loc. cit.*).

### 17.—THE THROAT MUSCULATURE<sup>1</sup>

In *Sphenodon*, the Chelonia, the Crocodilia, and the urodele Amphibia, the Mylohyoideus anterior and posterior are present as a continuous superficial layer (Fig. 38). In the Squamata this sheet is interrupted by interdigitation of the Geniohyoideus where the latter arises upon the median ventral border of the lower jaw. In the Sauria differences in number and size of the interdigitating bundles are noticeable among the various superfamilies. All the lizards have at least one interdigitating bundle separating the Mylohyoideus anterior and posterior. Many of the families have a number of regularly spaced bundles inter-

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<sup>1</sup>I have not been able to employ systematically the extensive morphological studies of Zavattari (1910) on the reptilian throat musculature.



lacing at definite intervals with the Mylohyoideus anterior. In most cases the lesser number of bundles is associated with certain complexities, undoubtedly secondary, in the form and divisions of the Mylohyoideus. Also the lesser number is usually present in those groups where wide separation, in space and in direction of fibers, occurs between Mylohyoideus anterior and posterior. This leads one to suppose that primitive saurian conditions are represented by a number, eight or more, of small, equal, regularly distributed interdigitating bundles of the Geniohyoideus and Mylohyoideus and by scarcely any separation between the anterior and posterior parts of the latter muscle.

Families in which these supposedly ancestral features remain are the:

Gekkonidæ: *Coleonyx variegatus*, Fig. 42.

*Gekko verticillatus*, Fig. 62.

Scincidæ: *Trachysaurus rugosus*, Fig. 49.

Gerrhosauridæ: *Gerrhosaurus zechi*, Fig. 52.

Lacertidæ: *Lacerta ocellata*, Fig. 50.

Teiidæ: *Tupinambis nigropunctatus*, Fig. 51.

In the specialized gekkonid *Uroplates* the Mylohyoideus anterior is very thin and aponeurotic. Its fibers run strongly fanwise and are concentrated at their origin, allowing few or no parts of the Geniohyoideus to insert through them. The Mylohyoideus posterior in each case is extremely thin and degenerate with fibers directed obliquely backward and largely covered superficially by a broad portion of the median terminus of the constrictor colli which extends forward to the hyoid corpus. It is widely separated from the Mylohyoideus anterior. Some similarities are shown to the diploglossids, *Pygopus* and *Lialis* (cf. Figs. 43 and 56).

The Iguania and Rhiptoglossa, with a few explicable exceptions, have the Mylohyoideus anterior in two layers. The fibers of the superficial layer in the Iguanidæ are directed transversely or obliquely backward (cf. Figs. 44 and 45). The fibers of the principal (profound) layer run transversely and obliquely forward from their origin. The superficial layer is developed from an anterior slip and never interdigitates with the Geniohyoideus. The principal layer represents the usual Mylohyoideus anterior of the Gekkota, and interdigitates by from one to six small bundles with the Geniohyoideus. In the iguanids, *Callisaurus*, *Uma*, and *Holbrookia*, alone, is the superficial layer absent. In these genera it is still amalgamated with the principal layer. Various stages of separation may be seen in the genera *Sceloporus*, *Chalarodon*, and



*Phrynosoma*. Further separation appears to occur in *Leiocephalus*, *Crotaphytus*, and *Dipso-saurus*. In *Anolis*, *Polychrus*, and *Basiliscus*, the superficial bundle is weak but well separate. In the "Cyclura group" comprising the genera *Iguana*, *Amblyrhynchus*, *Ctenosaura*, *Brachylophus*, *Sauromalus*, and *Cyclura*, the superficial bundle is very specialized and consists of definitely directed fibers not connected with the skin. Detailed resemblances are present in this group which I have outlined in manuscript and which will not be repeated here. Suffice it to say that the group appears to be a natural one, on the basis of the musculature with close resemblances prevalent between *Sauromalus* and *Cyclura*, and *Ctenosaura* and *Brachylophus*.

There is some evidence (e.g., number of cervical ribs) to show that *Holbrookia*, *Crotaphytus*, *Phrynosoma*, and *Sceloporus* are relatively primitive iguanids. If so regarded, we may perhaps consider the conditions of the throat muscles as primordial in these and related genera. This would be expected from the simplicity of the Mylohyoideus in *Holbrookia*, *Callisaurus*, and *Uma* and high number of interdigitations in some of these genera. Simple conditions are also present in *Chalarodon*, *Crotaphytus*, *Phrynosoma*, and *Sceloporus*. *Dipso-saurus*, *Uta*, and *Leiocephalus* possess closer resemblances to the *Cyclura* group than do the genera just mentioned.

Eight representative genera of agamids examined exhibit two layers in the Mylohyoideus anterior. It is evident from the relations with the Geniohyoideus that the superficial (principal) layer in the agamids and chameleons represents the profound (principal) layer in the iguanids, and that the profound layer is not present in the latter group. The superficial (principal) layer has the same direction as the profound (principal) layer in Iguanidæ, being transverse or anteriorly oblique. The profound layer is directed transversely and obliquely backward in both agamids and chameleons (cf. Figs. 46 and 47).

Among the agamid genera examined, *Liolepis belliana* appears to be the most generalized. Here the profundus is thin, restricted, and almost indistinguishable; there are four strong interdigitations with the Geniohyoideus and direct continuity persists between Mylohyoideus anterior and posterior. In *Agama colonorum* and *Physignathus lesueurii* the profundus is more advanced and the intersecting portion of the Geniohyoideus is smaller. In *Amphibolurus muricatus* the profundus is exceptionally broad and there are only two interdigitating bundles. In *Calotes* and *Japalura* a wide separation of anterior and posterior occurs with specialization of the former. In *Draco* there are many



singular features including the presence of a Depressor labii inferioris innervated by the mylohyoid nerve and unique among lizards so far as I know. There is but a single interdigitating slip and a considerable interspace is developed as in *Calotes*, *Amphibolurus*, and *Japalura*.

*Uromastix* has an extent and separation of parts almost exactly the reverse of what occurs in the cycluran iguanids.

Apparently in both agamids and iguanids a tendency is evinced for development of certain masticatory specializations. This involves separation of the fibers of the Mylohyoideus anterior apparently for pressure forward and upward, and backward and upward of the tongue upon the palate. The end result accomplished appears to be the same in the more specialized members of both families, but the derivation of the muscle fibers in the mechanism evolved is not identical and the direction of each resulting layer and bundle of the Mylohyoideus anterior becomes opposite in the two families (cf. Figs. 44 and 45 with Fig. 46).

It should be emphasized that the relations and appearance of the two layers of the Mylohyoideus anterior in *Chamæleon* are like those in the Agamidæ and not at all like any other lizards. This strengthens much other evidence of community in these two groups. In *Chamæleon gracilis* (Fig. 47), the Mylohyoideus posterior has vanished to a mere shred, and the area of the Constrictor colli is greatly extended forward beneath the posterior end of the Mylohyoideus anterior.

Among the Scincomorpha (except in amphisbænians) no great modifications of the throat muscles are found. An anterior cutaneous slip of the Mylohyoideus anterior is developed in the Scincidæ, Dibamidæ, Gerrhosauridæ, and Lacertidæ, but is lacking in the Xantusiidæ, Feyliniidæ, and Teiidæ (cf. Figs. 48-52).

The Amphisbænidæ are unique in pattern of throat musculature. The Cervicomandibularis has a broad insertion and, as in all strong burrowers, is enormously developed to act as a powerful depressor and lateral adductor of the head. The forward extension of Mylohyoideus posterior, likewise the longitudinal raphe in the Constrictor colli and the anterior separation of two parts of the Cervicomandibularis, recall the conditions in *Varanus* (cf. Figs. 40 and 54).

In the Varanidæ very peculiar modifications arise apparently in connection with the sutural break in the lower jaw. The Mylohyoideus posterior is specially developed and strong. It extends far forward over the nearly concealed Mylohyoideus anterior, and seems to be so placed as to exert a powerful action in swallowing and in pulling together the angles of the jaw. The Constrictor colli, a swallowing muscle, is enor-



mous and is divided into dorsal and ventral halves by a longitudinal raphe. The Geniohyoideus and Cervicomandibularis are both specially developed and by their pull would tend to spread the jaws when the mouth is open. The Cervicomandibularis in two divisions is attached to the lower jaw on the ventral side by a superficial fascia and profound supplementary tendons, controlling both halves of each ramus (cf. Fig. 54.)

The Anguioidea are distinguished by the possession of an anterior mandibular muscle similar to the Intermaxillaris of serpents and developed, as shown in *Gerrhonotus*, as a cutaneous attachment of the forward part of the Genioglossus. I have called this muscle the Genio-myoideus (cf. Figs. 58–61). It is present in all the Anguidæ, Xenosauridæ, and Anniellidæ I have examined and reaches its maximum development in *Heloderma*. It is absent in the Zonuridæ.

The Anguioidea are further differentiated by the presence of an anterior superficial reflected bundle of the Mylohyoideus anterior similar to that found in the cycluran iguanids. The pattern of the throat muscles of *Anniella pulchra nigra* and of *Gerrhonotus scincicauda webbia* is complex and almost identical; and equally close resemblances are seen between *Celestus costatus* and *Ophiodes striatus*. *Ophisaurus anguis* and *Anguis fragilis* are similar to each other and somewhat different from both *Ophiodes* and *Gerrhonotus*.

The Zonuridæ represent a moderately advanced stage in comparison with the Scincomorpha and Gekkota but a less complex type than other Anguimorpha (cf. Figs. 55 and 57). The Mylohyoideus is simple and undivided but the geniohyoid interdigitation is much restricted in both *Zonurus* and *Chamæsauro*. In *Zonurus* as in the Iguania the Geniohyoideus is divided, the median half inserting on the mid-ventral raphe and the external half in the usual position on the mandible (cf. Figs. 44, 45 and 55). In *Chamæsauro* the Geniohyoideus is single.

The Mylohyoideus, a breathing muscle in urodeles and Chelonia, has become highly specialized in certain lizards for masticatory and cutaneous functions.<sup>1</sup> In some groups the muscle is degenerate, but still shows signs of former specialization. In the strictly herbivorous forms, *Amblyrhynchus*, *Uromastix*, *Iguana*, *Dipsosaurus*, and *Sauromalus*, a thickening and increase of mass has occurred which has not apparently affected the pattern characteristic of the groups to which these lizards belong.

<sup>1</sup>In absence of a secondary palate (cf. p. 394) the Mylohyoideus anterior probably also serves to hold the tongue (floor of mouth in Varanidæ) closely up against the palate in order to allow the passage of air through the naso-pharyngeal canals during respiration.



## 18.—THE TONGUE

The shape and particularly the texture of the tongue have long been considered diagnostic of various groups of saurian families. Further investigations have upheld the importance of these features. Miss De Rooÿ (1915, Fig. 1) has illustrated certain examples of tongues among the Gekkota, Iguania, Scincomorpha, and Anguimorpha. Göppert (1903) figures others and shows the exact relation of the shape of the tongue to the fleshy and bony parts of the roof of the mouth.

The histological significance of the texture of the tongue in the major groups of lizards may be determined upon examination of the results of Seiller (1891, 1892). The papillæ of the Ascalabota and Diploglossa are delicate structures, developed apparently to give more surface for the epidermal glands which cover them as a continuous sheath of unspecialized glandular tissue. The papillæ of the Scincomorpha have produced a toughened, non-glandular tip, the glandular surfaces being restricted to the bases of the scale-like papillæ. The glands in *Lacerta* are of a more highly specialized type than those of *Anguis* and *Pseudopus*, making derivation of the papillate from the laminate and scaly forms improbable. Holl (1888) shows sections of the tongue in *Lacerta* similar to those Seiller has figured.

The broad, fleshy, partly smooth, partly papillate tongues of geckos and iguanids would seem histologically the least specialized and probably the more ancient type. It is impossible to regard the varanid and ophidian deeply bifid, sheath-based, tubular condition as anything but specialized. The tongue in these forms is highly extensile and functions externally as a tactile organ. Various stages illustrating the steps leading up to such a highly modified state may be seen in certain forms (Lacertidæ, Teiidæ, and Anguidæ) where the tongue functions both as a masticatory and as an external tactile organ. On this view the original, slightly nicked tip of the Ascalabota has become drawn out into two rather sharp points, the tongue surface has become smooth, thin, and folded to allow greater extensile capacity, the basihyal segment of the hyoid arch becomes more elongate, loosely articulated with the corpus, and in *Varanus* even separated from the rest of the hyoid apparently to allow more freedom of motion of the entire branchial apparatus.

The structure of the chameleon tongue comprises highly modified muscles, bones, and ligaments strictly comparable throughout with those of other lizards, and there is nothing to prevent the complex from having been acquired from an agamoid type of throat musculature (cf. Gandolfi, 1908). The highly extensile tongue has apparently been developed in



connection with the sloth-like movements of this extreme, arboreal, insectivorous type. The curious mechanism has been carefully studied by Kathariner (1895) and by Dewèvre (1895) who do not agree as to the *modus operandi*. The "pneumatic" theory of Dewèvre is not thoroughly acceptable since Germershausen (1913) has shown that many chameleons do not possess the laryngeal air sac necessary under his argument. (Cf. Fig. 47.)

### 19.—THE LOWER JAW

Certain of the elements of the reptilian lower jaw (cf. Gregory, 1913) are fused or absent in many families of lizards (cf. Figs. 107 and 112). Cope (1892a) has stated that the angular fuses with the articular (=articular+prearticular) in the Gekkonidæ, Feyliniidæ, *Acontias*, the Anniellidæ, and Amphisbænidæ. Bedriaga (1884) finds only four elements in *Blanus cinereus*.<sup>1</sup> Baur (1894) recognizes five elements in *Anniella*—"the articular and supra-angular being ossified." Coe and Kunkel (1906) support the observations of Baur. The splenial is small or absent in Agamidæ and absent in Chamæleontidæ; being well-developed in other families. In the Chamæleontidæ the dentary enlarges to take the place of the splenial. The articular, prearticular, and surangular have fused in the advanced chamæleontid *Brookesia* (cf. Siebenrock, 1893a, Pls. I and II). In *Xantusia* but three bones remain, "the articular [=articular+prearticular] angular, and surangular are coössified, and the splenial and dentary."

According to Boulenger (1885, p. 239) the mandible consists of only four bones in the Pygopodidæ, "the angular, surangular, and articular [=articular+prearticular] having coalesced." Only three elements remain in *Ophioseps*, Jensen (1901).

In the Uroplatidæ (cf. Siebenrock, 1893b, Pl. xiv) only five bones are present, the articular and prearticular, and the surangular and angular being fused.

In some Lacertidæ (cf. Siebenrock, 1894) the splenial is exceptionally large.

The articular and prearticular are fused in all adult lizards I have examined or seen figured. They are separate in the Cotylosauria and Pelycosauria, and in the embryo of *Sceloporus* (Kingsley, 1905).

Fusion between the prearticular and surangular seems to be an age character in *Lygosoma* and *Tupinambis*, and we cannot naturally attach as much phylogenetic importance to fusions as to such absence and reduction as occur in the subterranean forms and in the agamids and chameleons.

<sup>1</sup>Apparently there are only three in *Agamodon*, Peters (1882).



## 20.—THE CAUDAL CHEVRONS

Caudal chevrons are intercentral (cf. Boulenger, 1891, p. 114, 115) in most lizards including all the Ascalabota, most of the Scincomorpha, and the more primitive Anguimorpha. The intercentral position is unquestionably the original one. In the Anguimorpha alone is there any strong tendency for central attachment and in this group such union always seems to occur by progressive anterior migration of the chevron base (intercentrum).

In the teiid, *Tupinambis*, there is an apparent tendency toward central attachment by posterior migration (cf. Boulenger, *loc. cit.*, Fig. 4) but the attachment itself has not yet been developed. In the degenerate scincomorph, *Dibamus*, chevrons are absent.

In the less specialized Anguimorphs, *Zonurus*, *Gerrhonotus*, and *Heloderma*, intercentral attachment still occurs with a tendency to forward migration (cf. Figs. 99–101). In *Ophisaurus*, *Anguis*, and *Anniella* the chevrons are fused centrally as they are in the Serpentes. In *Xenosaurus*, *Chamæsauro*, and *Lialis* they are unfused and intercentral. Among the Glyptosauridæ, the Eocene forms (cf. Fig. 101) have a posterior central attachment, the Oligocene *Helodermoides* possibly a more advanced central situation. For this reason and because of the highly specialized body scutes and fused frontals, I do not derive *Heloderma* directly from the known Glyptosauridæ. Among all the Platyntota nearly mid-central attachments occur. *Varanus*, *Saniwa*, *Thinosaurus*, and *Tylosaurus* are alike in having such a location and in the pediculate articulation of the chevrons.

## 21.—THE OS INTERMEDIUM

The intermedium is always small and frequently absent in the Sauria. It seems to be sporadically present among primitive families but is entirely absent as far as known in the Gekkota. Its loss seems usually to occur through fusion with the neighboring ulnare which sometimes provides a pocket for its reception. It is large in *Sphenodon* and in many fossil reptiles, including *Aræoscelis* (Williston, 1914, p. 128 and Fig. 2F).

It appears only in scattering genera for the most part, but what is known of its distribution seems significant—namely that families (except the gekkonoids) considered primitive in other respects all have some genera with an ossified intermedium present as a separate element in the adult. Cope (1892*a*, p. 196) indicates that the intermedium was present in all genera at his disposal (*Phyllodactylus*, *Coleonyx*, *Anolis*, *Dipso-saurus*, *Sauromalus*, *Crotaphytus*, *Sceloporus*, *Phrynosoma*, *Gerrho-*



*notus*, *Cnemidophorus*, *Xantusia*, and *Eumeces*). I have examined all these except *Dipso-saurus*, *Cnemidophorus*, and *Eumeces* with results as indicated below.

The intermedium is present in:

Xantusiidæ (*Xantusia vigilis*, Noble, 1921, p. 15); Scincidæ (*Tiliqua*, A. M. N. H., *Eumeces schneideri*, cf. Siebenrock, 1895a, p. 33, *Chalcides ocellatus*, Born, 1880); Lacertidæ (all species examined by Born, 1876, and Siebenrock, 1894); Teiidæ (*Tupinambis nigropunctatus*, A. M. N. H., *Tejastejuexin* and *Ameiva vulgaris* Born, 1876); Helodermatidæ (*Heloderma*, A. M. N. H., cf. also Troschel, 1853); Anguidæ (*Gerrhonotus*, A. M. N. H. 9159); Zonuridæ (*Zonurus giganteus*, A. M. N. H.).

In some Gerrhosauridæ (cf. *Zonosaurus*, Siebenrock, 1895, Fig. 8) the intermedium appears to be joined by suture to the ulnare. In the following genera it is fused with the ulnare or absent entirely: according to Hoffmann (1890) in *Phyllodactylus lesueuri*, *Lygosoma*, *Seps chalcides*, and *Draco viridis*; according to Siebenrock (1893b) in *Uroplates*, (1895a) in most Scincidæ, including most species of *Chalcides*, and certain Gerrhosauridæ and Anguidæ.

I have found it lacking in *Coleonyx* and many other gekkonoids, in the scincs *Trachysaurus* and *Egernia*, in the degenerate teiid *Bachia* (Fig. 68a), in *Varanus*, in *Xenosaurus*, in the iguanids *Crotaphytus*, *Anolis*, *Sceloporus*, *Phrynosoma*, *Sauromalus*, *Cyclura*, and *Iguana*, in the agamid *Calotes*, and in *Chamæleon gracilis* and *C. vulgaris*.

Brühl (1875–1888) in copying a figure of Born (1876) wrongly interprets one of the palmar sesamoids of *Chamæleon* as an intermedium. This error has gained a place in subsequent literature, although Born himself (1880) has called attention to it. Born also reports the intermedium in *Gonocephalus dilophus*.

Born (1876) derives the *Chamæleon* foot from that of other lizards. Stecker (1877) thinks this improbable and believes that *Chamæleon* represents the primitive type from which others have been modified. He finds the intermedium present in the very young embryo of *Chamæleon senegalensis* as a tiny cartilage. There seems nothing but this obscure evidence to support Strecker's opinion.

## 22.—THE BODY MUSCULATURE

The Rectus abdominis muscle in autarchoglossid lizards can usually be subdivided into four parts (cf. Maurer, 1896). Of these only two are generally present in the Ascalabota (cf. Schneider, 1879; Gadow, 1882). These parts comprise (cf. Figs. 40, 62–66, 68, and 75): (1) the Rectus



profundus or main median portion of the Rectus, segmented, in contact on each side with the Obliquus externus profundus and homologous anteriorly with the substernal longitudinal muscles; (2) the Rectus medianus, segmented, often intimately connected with the skin over the whole belly and aiding in locomotion by its pull on the ventral scales; (3) the Rectus lateralis, unsegmented, and forming the lateral continuation of the Rectus medianus; (4) the Rectus internus, unsegmented, arising on the pubis and passing forwards sometimes as far as the sternum and dorsal to the Rectus profundus. The first and last subdivisions need not further concern us. The medianus and lateralis may together be called the Rectus superficialis and as such have an important bearing on taxonomy and saurian evolution.

The Rectus lateralis is found only in lizards. According to Maurer (1898) it arises in the embryo of *Lacerta* as the lateral portion of the superficial layer of the Rectus abdominis. The muscle may usually be recognized by its position alongside the Rectus medianus and profundus and between the Obliquus externus superficialis and the median portion of the Obliquus externus profundus (cf. Figs. 63 and 64). It is unsegmented and in the limbed Autarchoglossa may be distinguished by the fact that it passes ventrally over the superficial surface of the Pectoralis to insert into the skin beneath the shoulder girdle or near the axilla. It is sometimes continuous by fascia, below the Pectoralis, with the sterno-cleido-mastoid and sterno-hyoid muscles. It is often closely joined to the skin and seems in these cases to function very strongly in jerking the body forward, assisting the limbs (Lacertidæ, Teiidæ). It is absent as a separate muscle in the limbless lizards, here being fused indistinguishably with the Rectus medianus to form the Rectus superficialis.

The Rectus medianus is comparable with the Rectus superficialis so-called of *Sphenodon* and in lizards the fibers join the parasternal bars, when the latter are present, in the same way as in *Sphenodon*. The Rectus medianus develops in *Lacerta* (Maurer, *loc. cit.*) by splitting from the main Rectus profundus at an early stage and it seems usually to maintain its individuality because of its connections and functions as a skin-muscle. It gives off the unsegmented Rectus lateralis extending out between the Obliquus externus superficialis and the Obliquus externus profundus. It is covered superficially by the terminal fibers or fascia of the Obliquus externus superficialis. It arises on the pubis and passes forward only to the sternum. It receives upon its dorsal surface the scalares bundles arising on the tips of the ribs. These bundles



are absent in the Iguania and Rhiptoglossa and are usually reduced in the Gekkota. Here they join the inscriptions of the Rectus profundus.

The parasternum develops on the ventral surface of the Rectus superficialis and the true ribs, in order to join the parasternal bars, are usually forced (as in *Sphenodon*) to pass up through the fibers of the Rectus profundus.

In the limbed Autarchoglossa the Rectus superficialis is divided into median and lateral portions; in the limbless forms the two parts cannot be separated and the whole muscle continues as a band on each side as far forward as the terminus of the sterno-cleido-mastoid and sterno-hyoid muscles, from which it is separated by an inscription or by the presence of the reduced sternum or clavicle (cf. Figs. 40 and 75). In the highly subterranean Scincoidea the Rectus superficialis becomes reduced to a narrow strip on each side hidden beneath the overgrowth of the enormous Obliquus externus superficialis. In the degenerate teiids and the Amphisbænidae it is attached to the skin (cf. Figs. 40 and 68). In the grass-inhabiting, surface-terrestrial, limbless anguids it is broadened and almost inseparably joined with the ventral scales. In the Pygopodidae and Chamæsauridae, it is developed as a broad ribbon on each side of the mid-line and is not closely connected with the skin.

I have not been able to find any trace of the Rectus superficialis in any of the ascalabotids examined, with the exception of three genera of terrestrial Agamidæ (*Uromastix*, *Physignathus*, and *Liolepis*) where the Rectus lateralis continues forward over the Pectoralis (cf. also Sanders, 1872, and Fürbringer, 1875). I have seen it in all the Autarchoglossids investigated, including representatives of all families except the Anelytropidae.

It is absent in the following genera:

#### Gekkota

*Ptyodactylus* (Gadow, 1882), *Thecadactylus rapicauda*, *Gekko verticillatus*, *Coleonyx variegatus*, *Hemidactylus brookii*, *Uroplates fimbriatus*, and *Platydictylus japonicus* (Sanders, 1870).

#### Iguania

*Uma notata*, *Chalarodon madagascarensis*, *Crotaphytus collaris baileyi*, *Crotaphytus wislizenii*, *Phrynosoma hernandesi*, *Phrynosoma coronatum* (Sanders, 1874), *Sceloporus magister*, *Uta thalassina*, *Dipsosaurus dorsalis*, *Sauromalus hispidus*, *Amblyrhynchus cristatus*, *Basiliscus vittatus*, *Anolis cuvieri*, *Polychrus marmoratus*, *Enyalius rhombifer*, *Enyalioides heterolepis*, *Stenocercus boettgeri*, *Liolaemus multiformis*, *Leiocephalus*



*carinatus* (and, according to Gadow [1882], in *Iguana* and *Ophyroessa*); in the agamids, *Amphibolurus muricatus*, *Lophura amboinensis*, *Japalura swinhonis*, *Calotes versicolor*, and *Draco formosus* (cf. also Lafrenz, 1914).

#### Rhaptoglossa

*Chamæleon gracilis*, *Chamæleon vulgaris*.

The Rectus superficialis is present in the following:

#### Iguania

*Uromastix hardwickii* (cf. Fürbringer, 1875), *Physignathus lesueurii*, and *Liolepis belliana* (cf. Sanders, 1872).

#### Scincomorpha

*Xantusia riversiana*, *Trachysaurus rugosus*, *Dasia smaragdinum*, *Plestiodon quinquelineatum*, *Chalcides ocellatus*, *Chalcides sepoides*, *Chalcides tridactylus*, *Acontias meleagris*, *Feylinia currori*, *Dibamus novæguineæ*, *Gerrhosaurus zechii*, *Lacerta ocellata*, *Tupinambis nigropunctatus*, *Bachia intermedia*, *Cnemidophorus* sp.?, *Amphisbæna alba*, *Rhineura floridana*.

#### Anguimorpha

*Varanus nuchalis*, *Lialis burtoni*, *Pygopus lepidopus*, *Heloderma suspectum*, *Xenosaurus grandis*, *Gerrhonotus scincicauda webbiai*, *Ophisaurus apus*, *Anguis fragilis*, *Ophiodes striatus*, *Anniella pulchra nigra*, *Zonurus giganteus*, and *Chamæsauro macrolepis*.

There are other body muscles reduced or absent among the Ascalabota and present in the Autarchoglossa. Of the Intercostales ventralis (part of Int. internus), the special slips (Scalares) which run downward into the Rectus are absent in all iguanids and agamids I have examined and in the chameleons; they are never so greatly developed in geckos as in autarchoglossids and are absent in *Uroplates*. The Intercostales externi longi, constituting those parts of the Intercostales externi which skip over the ribs, are absent in all iguanids and most agamids and in chameleons, but are often present in geckos. The Obliquus externus profundus is absent or reduced in iguanids, in some agamids, and is absent in chameleons and in *Uroplates*.

The Intercostales externi longi, present in all the Autarchoglossa, are most powerfully developed in the limbless forms where the ribs are used for walking and burrowing.

Fürbringer (1869), when investigating the anatomy of degenerating limbs, unfortunately paid little attention to the much more significant



changes in the body muscles in limbless lizards. He recognized no subdivisions of the Rectus abdominis except those in *Pseudopus* (= *Ophisaurus*); he distinguished the Rectus lateralis under the name Suprapectoralis as Rüdinger had done (cf. Fürbringer, 1875).

Schneider (1879) was apparently the first to appreciate the important variations of the body muscles of the Sauria. He drew up an outline of classification based upon muscle characters but too few facts were at his disposal for the expression of any significant generalizations. He recognized the absence of the Scalares in the Iguanidæ, Agamidæ (Chamæleontidæ?) and in the gekkonid *Platydictylus*; he noticed the great reduction of the Rectus in chameleons without knowing of the almost equal reduction in *Uroplatus*; and he commented upon the decreasing number of myocomata in the Rectus abdominis of certain iguanids and especially among agamids.

Gadow (1882) described certain divisions of the Rectus including the Rectus lateralis (the latter he observed to be absent in the genera *Ptyodactylus*, *Iguana*, *Ophryoesa*, *Polychrus*, *Phrynosoma*, and *Chamæleon*). His view of the innervations and "visceral" origin of the muscle and of the nature of the Rectus internus have been shown by Maurer to be incorrect but he noticed the important variations of the Rectus superficialis.

Maurer (1896, 1898) has most thoroughly studied the body muscles of certain reptiles and amphibians both from comparative and embryological points of view. The conclusions he reaches regarding the origin of the various layers present in lizards are important enough to warrant summary here.

The ventral body musculature in reptiles is innervated segmentally by the ventral branches of the spinal nerves. The Rectus itself is formed from the more dorsal layers and cannot be considered "visceral musculature," as Gadow and Schneider have stated. There is no genetic basis for Müller and Huxley's divisions—the episkeletal and hyposkeletal musculature—the more logical distinction is between the dorsal musculature innervated by dorsal branches of the spinal nerves and the ventral musculature with which we are dealing.

The ventral musculature arises from the ventral half of the mesodermic muscle plates, and these at a very early stage develop two layers of primordial muscle cells supposedly corresponding to the two layers of side muscles found in fish and in *Cryptobranchus*.

The outside layer develops into the entire group of muscles lying over the ribs, including the Intercostalis externus. The inside layer forms



the Intercostalis internus, the Obliquus internus and the Transversus, as had already been suspected from comparative data. The Rectus develops from both layers during their growth downward around each side of the body. The layers which contribute to it are shown in the following diagram.

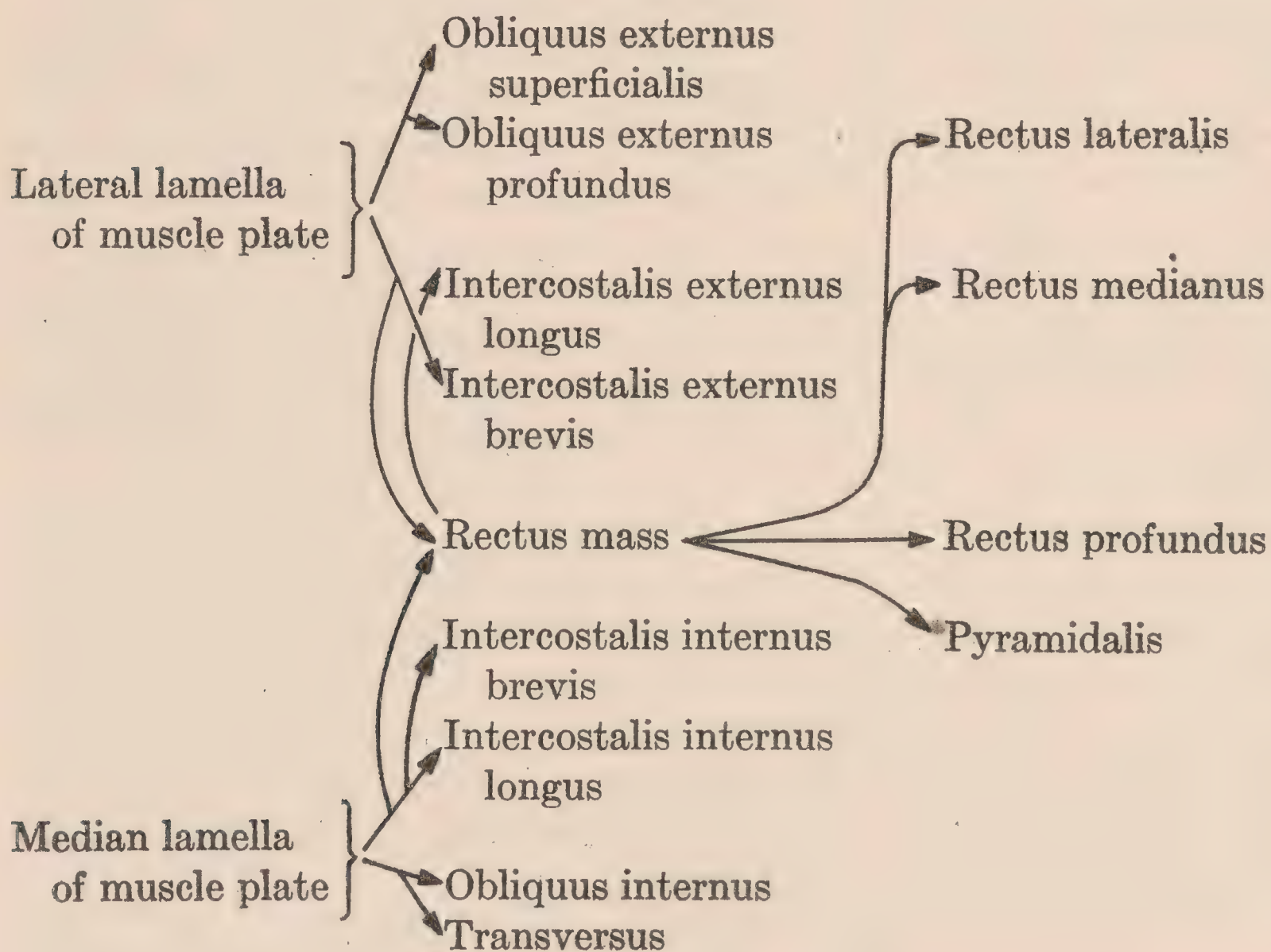
# THE EMBRYOLOGICAL DEVELOPMENT OF THE RECTUS ABDOMINIS

## EMBRYO OF *Lacerta agilis*

First Stage

Second Stage

Third Stage





# THE COMPARATIVE MORPHOLOGY OF THE RECTUS ABDOMINIS

## RAMI VENTRALES OF NERVI SPINALES

| Primary Layers<br>As in <i>Cryptobranchus</i><br>and embryo<br><i>Lacerta</i> | <i>Triturus</i>                                                                                                                                                         | Crocodile                                                                                                                      | <i>Sphenodon</i>                                                                                 | <i>Lacerta</i><br>(Autarchoglossid)                                                        | <i>Chamaeleon</i><br>(Ascalabotid)                                       |
|-------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|
| Obliquus<br>externus                                                          | <div> <div>Rectus profundus<br/>(weak in adult,<br/>strong in larva)</div> <div>↓</div> <div>Rectus superficialis<br/>(strong in adult,<br/>weak in larva)</div> </div> | <div> <div>Rectus profundus</div> <div>Truncocaudalis<br/>(a swimming<br/>muscle)</div> <div>Rectus superficialis</div> </div> | <div> <div>Pyramidalis<br/>(=Rectus internus<br/>Gadow)</div> <div>Rectus profundus</div> </div> | <div> <div>Pyramidalis</div> <div>Rectus profundus<br/>(sometimes<br/>absent)</div> </div> | <div> <div>Sometimes<br/>absent</div> <div>Rectus abdominis</div> </div> |
| Obliquus internus                                                             |                                                                                                                                                                         |                                                                                                                                |                                                                                                  |                                                                                            |                                                                          |
|                                                                               |                                                                                                                                                                         |                                                                                                                                |                                                                                                  |                                                                                            |                                                                          |
|                                                                               |                                                                                                                                                                         |                                                                                                                                |                                                                                                  | Rectus medialis                                                                            | Absent                                                                   |
|                                                                               |                                                                                                                                                                         |                                                                                                                                |                                                                                                  | Rectus lateralis                                                                           | Absent                                                                   |



# THE COMPARATIVE MORPHOLOGY OF THE VENTRAL BODY MUSCLES IN LOWER VERTEBRATES

| RAMI VENTRALES OF NERVI SPINALES                              |                                                      |                                     |                                       |                                 |
|---------------------------------------------------------------|------------------------------------------------------|-------------------------------------|---------------------------------------|---------------------------------|
| Fish and<br><i>Cryptobranchus</i>                             | <i>Triturus</i> larva                                | Crocodile                           | <i>Sphenodon</i><br>(Autarchoglossid) | <i>Lacerta</i><br>(Ascalabotid) |
| COURSE OF RAMI LATERALES OF VENTRAL BRANCHES OF SPINAL NERVES |                                                      |                                     |                                       |                                 |
| Obliquus externus                                             | Obliquus externus superficialis                      | Same                                | Same                                  | Same                            |
|                                                               | Obliquus externus profundus                          | Same                                | Same                                  | Absent                          |
|                                                               |                                                      | Absent                              | Intercostales externi longi           | Absent                          |
|                                                               |                                                      | Intercostales externi breves        | Same                                  | Same                            |
|                                                               | Rectus                                               | Same                                | Same                                  | Same                            |
| Obliquus internus                                             |                                                      | Intercostales interni breves        | Same                                  | Same                            |
|                                                               |                                                      | Intercostales interni longi         | Same                                  | Absent                          |
|                                                               |                                                      | Same                                | Same                                  | Absent                          |
| COURSE OF VENTRAL SPINAL BRANCHES                             |                                                      |                                     |                                       |                                 |
| Transversus (segmental in <i>Cryptobranchus</i> )             | Subvertebrales                                       | Intercostales interni dorsali longi | Same                                  | Same                            |
|                                                               |                                                      | Same                                | Same                                  | Same                            |
|                                                               | Transversus (unites with obliquus internus in adult) | Same                                | Same                                  | Same                            |
|                                                               |                                                      |                                     |                                       | (secondarily segmental)         |



It is apparent from Maurer's results that the *Rectus superficialis* is a morphologically widespread and embryologically precocious muscle. Its absence in *Ascalabota* cannot well be due to the primitiveness of that group but more probably to the fact that all forms in the group except certain primitive agamids have lost the muscle, while it remains and develops in the *Autarchoglossa*. This would seem to imply that the pro-Sauria may have carried the body close to the ground and that this mode of locomotion has been correlated with the development of "slinking" musculature in the belly-wall.

Lizards today which retain this mode of locomotion retain the musculature, while the group that seems to have early adopted arboreal life has apparently lost the musculature in question and carries the body more stiffly and sometimes held up off the ground. Even the thoroughly terrestrial and non-lamellate geckos carry the body well elevated. Depressed geckos are mostly arboreal. Compressed Iguania are all arboreal and carry the body elevated. Depressed Iguania are always terrestrial but generally elevate the body when running in contrast to the scincs, lacertids, teiids, and anguids, where the belly usually remains in closer contact with the earth.

Whatever has happened, it seems clear that the method of locomotion attained by the *Autarchoglossa* preserves a key system of highly developed body muscles opening up a treasure-chest of possibilities when opportunity for preservation of a worm-like burrowing, or a limbless, snake-like, grass-living, habitus is afforded by the environment. Time and again in various parts of the world scincs, teiids, and anguids appear to have gone off on such a course, lost the limbs and girdles in varying degree, and developed even more highly, and in a number of different ways, sets of muscles already present in their more normal ancestral forms. The ascalabotids constitute half of the entire lizard population of the world. They have never developed limbless, burrowing genera and seemingly cannot do so on account of the arboreal specializations and reductions in their locomotory musculature.

If for any reason whatever the limbs should degenerate in geckos and iguanians the lizards would find themselves helpless; if, however, such a thing happened in a scincoid or anguimorph (as indeed it seems to be happening in frequent instances) the creature finds itself still capable of locomotion, and if grass-land or humus-soil environments happen to be at hand, such limb reduction may become favorable.



## 22a.—The Parasternum and its Relations to the Xiphisternum and Sternum.

The parasternum, constituting the so-called abdominal ribs, seems to be developed separately from the sternum chiefly among arboreal and in burrowing genera. It reaches a maximum extent among the subterranean Scincoidea (Fig. 75). It also appears in a slight degree among all known surface-living terrestrial Scincoidea, and, so far as known among the Anguimorpha,<sup>1</sup> only in the Chamæosaurinæ. It is most highly specialized in certain burrowing Teiidæ (Fig. 68). I have recognized it in the Uroplatidæ, a few iguanids, the Chamæleontidæ, the Scincidæ, the Feyliniidæ, and the Dibamidæ, in a teiid, *Bachia*, and in the zonurid, *Chamæsaura*. It has not previously been noted in the Dibamidæ and Zonuridæ. Stannius (1856) has mentioned the presence of abdominal ribs in *Platydictylus guttatus*. I have not found the parasternum in any of the gekkonid genera at my disposal.

In the Iguanidæ "abdominal ribs" are present according to Boulenger in the terrestrial genera, *Hoplocercus*, *Ctenosaura* (1 pair), *Cyclura* (1 pair), *Hoplurus*, *Chalarodon*, and *Liosaurus*, and in the arboreal genera *Iguana* (1–2 pairs), *Leiocephalus*, *Scartiscus*, *Urostrophus*, *Anisolepis*, *Enyalius*, *Enyalioides*, *Polychrus*, *Tropidodactylus*, *Norops*, *Anolis*, *Xiphocercus*, and *Chamæleolis*.

Siebenrock (1895a) notes the "costæ abdominalis" in *Chalcides tridactylus* (9 complete pairs), *C. mionecton* (5 pairs), *Ablepharus pannonicus* (4 pairs) and from one to three pairs in the rest of the scincid genera he examined. "Den Gerrhosauriden und Anguiden fehlen sie ganzlich."

Rabanus (1906–1915) figures sixteen pairs of parasternalia in the scincid, *Voeltzkowia mira*.

The number of parasternal ribs present in various genera is indicated below. Comparisons are given in order to illustrate the progressive increase in the number of parasternal ribs in series of autarchoglossine forms having a progressively burrowing habitus.

|                                   | Habitat      | Digits | Parasternal Ribs |
|-----------------------------------|--------------|--------|------------------|
| Ascalabota                        |              |        |                  |
| <i>Uroplates fimbriatus</i>       | Arboreal     | 5      | 13               |
| <i>Chalarodon madagascarensis</i> | Terrestrial  | 5      | 3                |
| <i>Brachylophus fasciatus</i>     | Arboreal (?) | 5      | 2                |

<sup>1</sup>It should be noted that both *Lialis* and *Anniella* and other snake-like anguids lack parasternal ribs in spite of their degenerate habitus. This may lend additional support to the view that the Pygopodidæ are diploglossids.



|                                                      | Habitat                | Digits            | Parasternal<br>Ribs                        |                     |
|------------------------------------------------------|------------------------|-------------------|--------------------------------------------|---------------------|
| <i>Cyclura</i>                                       | Terrestrial            | 5                 | 1                                          |                     |
| <i>Ctenosaura</i>                                    | Terrestrial            | 5                 | 1                                          |                     |
| <i>Iguana</i>                                        | Arboreal               | 5                 | 2                                          |                     |
| Anoline iguanids (Cope,<br>1892a)                    | Arboreal               | 5                 | 4-5                                        |                     |
| Polychrine iguanids<br>(Cope, 1892a)                 | Arboreal               | 5                 | 7-10                                       |                     |
| <i>Chamæleon vulgaris</i>                            | Arboreal               | 5                 | 11                                         |                     |
|                                                      | Habitat                | Digits            | True Ribs<br>After Sieben-<br>rock (1895a) | Parasternal<br>Ribs |
| Autarchoglossa                                       |                        |                   |                                            |                     |
| Scincomorpha                                         |                        |                   |                                            |                     |
| <i>Trachysaurus rugosus</i>                          | Surface<br>terrestrial | 5                 | 32                                         | 7                   |
| <i>Tiliqua scincoides</i><br>(Beddard, 1904b)        | Surface<br>terrestrial | 5                 | 34                                         | 7                   |
| <i>Ablepharus pannonicus</i><br>(Siebenrock, 1895a)  | ?                      | 5                 | 28                                         | 4                   |
| <i>Chalcides ocellatus</i>                           | Surface<br>terrestrial | 5                 | 37                                         | 2                   |
| <i>Chalcides mionecton</i><br>(Siebenrock, 1895a)    | Burrowing?             | 4                 | 44                                         | 5                   |
| <i>Chalcides sepoides</i>                            | Burrowing              | 3-4               | ?                                          | 14                  |
| <i>Chalcides tridactylus</i>                         | Burrowing              | 3                 | 58                                         | 9 <sup>1</sup>      |
| <i>Voeltzkowia mira</i><br>(Rabanus, 1906-15)        | Burrowing              | 0                 | ?                                          | 14-17               |
| <i>Acontias niger</i><br>(Fürbringer, 1900)          | Burrowing              | 0                 | ?                                          | 23                  |
| <i>Acontias meleagris</i>                            | Burrowing              | 0                 | ?                                          | 23                  |
| <i>Typhlosaurus auranticus</i><br>(Fürbringer, 1900) | Burrowing              | 0                 |                                            | 27                  |
| <i>Feylinia currori</i>                              | Burrowing              | 0                 |                                            | 35+ <sup>2</sup>    |
| <i>Bachia intermedia</i>                             | Burrowing              | 3-4 (cf. Fig. 68) |                                            | 13                  |
| <i>Chamæsauro macro-<br/>lepis</i>                   | Surface<br>terrestrial | 1-2               |                                            | 9                   |

<sup>1</sup>Carlsson (1887) has counted fifteen in this species.<sup>2</sup>Some irregular pieces (cf. also Müller, 1900 and Rabanus, 1906-15, who find the same number).



Schneider (1879) was perhaps the first to demonstrate, by the muscular connections, the different nature of what he called the true ribs and the belly ribs in *Anolis* and *Polychrus*, but he believed the condition here to be unlike that in the Chamæleons.

Gadow (1882) taking into account the absence of the Rectus considers the abdominal ribs of *Anolis* and *Chamæleon* "fully homologous" and takes issue with Schneider on this point. But Gadow did not distinguish the belly ribs from the true ribs; in other respects I should confirm his view.

Fürbringer's opinion of the so-called abdominal ribs of certain lizards was stated in 1900 (p. 249) about as follows: The abdominal or metasternal ribs following the sternum show various relations—they either end freely at different distances from the ventral mid-line, or they are bound together only by ligaments, or they join more or less intimately in the mid-line by their long terminal cartilages (abdominal ribs). . . . Sometimes these are cartilaginous sometimes calcareous. Also, ossified and partly independent abdominal ribs may form what might be thought to be a rudimentary parasternalia. Abdominocostalia still both united to the ribs and separated from them can be found together in the same animal. I have no definite views regarding these conditions and consider further accurate investigation necessary to decide the question (translation).

After this time Beddard (1904*a*, 1904*b*, 1906) published some accounts of supposedly special conditions in the Australian scincs *Tiliqua* and *Trachysaurus*, and believed that in these forms he could demonstrate the presence of a definite parasternum comprising the free lateral "abdominal ribs" overlapping at certain points the cartilaginous tips of the dorsal ribs lying in the deeper musculature.

He makes it clear, however, that he does not mean to extend the term parasternum to include all the so-called mid-ventral abdominal ribs but only those free lateral ribs included in the two special cases mentioned. Concerning the case in *Trachysaurus* where a pair of true ribs meet and fuse in the mid-line a little way behind the sternum, he says (1906): "These true ribs meet and fuse superficially and exactly resemble the succeeding abdominal ribs, so far as the median region is concerned. This, however, can invalidate no homology, for . . . the remaining pieces of cartilage so entirely overlap so considerable a portion of the true ribs that they [the cartilages?] cannot possibly be regarded as the equivalent of their [the cartilages?] median ventral extremities, which, indeed, themselves reach to within a millimetre or two of the



ventral middle line." Earlier than this he states (1904b): "It is to my mind possibly a matter for further inquiry as to how far the median ventral region of the post-sternal ribs which actually meet each other behind the sternum may not be actually a parasternum fused with true ribs." Williston (1916. p. 187) regards with favor this suspicion, saying: "We know of no fossil form in which the anterior or any dorsal ribs met or even approached each other in the middle or behind" the median coracoids. And Williston carries these observations to the logical inference that with the support of other paleontological evidence the sternum itself may be regarded as derived from such a parasternal apparatus as is represented in *Ophiacodon*.

It is of importance, therefore, to determine the morphology of the parasternum in lizards and to try and decide the question left open by Fürbringer as to whether all mid-ventral rib elements can be considered as true parasternalia. I think that the following summary of evidence will lead to the definite answer that in all cases both mid-ventral and free lateral parts of the abdominal ribs, when present, should be regarded as portions of a true parasternum.

We shall consider the following points in respect to the mid-ventral elements: (1) Their relations to surrounding soft tissues; (2) their relations to the true ribs; (3) their relations to the so-called xiphisternal rods and to the sternum; (4) their distribution and relations during development in a series of progressively degenerating species of a single genus; (5) comparisons with *Sphenodon*, crocodile, and more ancient forms.

(1)

In the following discussion of the myological relations of the parasternum, the muscle names proposed by Maurer (1896) are employed (cf. p. 377). The Rectus, it should be remembered, is almost absent in the chameleons and in Uroplates, so that the true relations appear only at the extreme posterior part of the abdomen where the Rectus is present. With this in mind we may say that the parasternum in lizards INVARIABLY lies ventral to the main Rectus profundus in the tissue between that muscle and the median terminal fascia of the Obliquus abdominis superficialis. The muscle sheet developed as the superficial layer of the Rectus abdominis, i.e. Rectus superficialis, is the muscle most closely attached to the median parasternum and fibers of the fascia of the superficial obliquus usually insert upon it (cf. Figs. 68 and 75). It must be emphasized that the parasternum never lies ventral to the superficial obliquus nor dorsal to the Rectus profundus. The first relation would allow a strictly dermal



origin which has probably not occurred (p. 392). The second would imply primitive association with the ribs, which is undoubtedly erroneous.

In autarchoglossid lizards, but not in *Sphenodon*, the lateral portion of the Rectus superficialis extends outward over the surface of the Obliquus abdominis profundus, the Intercostalis externus longus, and the extremities of the true ribs; and the ends of the true parasternal bars may extend out into this Rectus lateralis to overlap the terminal cartilaginous rib ends in the way noted by Beddard in the Australian scincs. I have seen this also in *Chalcides sepoides* and such a situation does not appear to be common.

The parasternal bars in lizards usually correspond exactly with the inscriptions of the Rectus and are never more numerous except where the Rectus is absent. Also, it is important to note, the parasternum never extends forward over the sternum and xiphisternum although the Rectus lateralis, in which it is sometimes developed, often does so.

(2)

The parasternal chevrons always correspond in position to the ribs but rarely extend caudalwards as far as do the dorsal ribs. Only in *Chamæleon* and *Uroplates* does this occur but even here the most posterior parasternal bars never gain a pleural articulation. The parasternal bars usually join the cartilaginous rib-ends directly, but connections are frequently lacking in the posterior region, are often anomalous and misplaced, and in cases where the parasternum extends laterally into the Rectus lateralis, the rib-tips may join the bars medially.

The parasternum of lizards does not therefore appear to be either primitively or ontogenetically related to the ribs. This is exactly what appears in the embryology of *Sphenodon* (cf. Schauinsland, 1903).

(3)

There is however a very specific relation of the parasternal bars to the xiphisternum and possibly also to the sternum. The position in the muscles is identical if we may accept Maurer's view that the sternocosto-coracoid muscles are certainly the disconnected, forward continuations of the Rectus profundus. These longitudinal muscles lie immediately dorsal to the sternum and represent that anterior continuation of the Rectus above the sternum which is found in the urodeles. Also, as the sternum and xiphisternum degenerate, in the limbless lizards, they gain more and more the appearance of the parasternal chevrons so that in some extreme degenerates (cf. *Dibamus*, Fig. 75; *Feylinia*, Fig. 73) the resemblance is nearly perfect. Furthermore, when anomalies occur



in the attachments of the sternum and xiphisternum to the ribs, the contiguous parasternal bars may show close affiliation with parts of the xiphisternal apparatus. Such a case is illustrated (Fig. 68). Here a true, highly modified parasternal bar, (P), has been made over on one side into a xiphisternal rod while its opposite half remains in normal condition. A parasternal element is apparently used to help "balance" assymetry in the xiphisternal apparatus and close serial homology of the structure is indicated.

## (4)

Further support for the theory of the independence of the parasternum in lizards may be obtained from a comparative study of the conditions in a group of closely related degenerating scincs. Such a series is available in the genus *Chalcides* (cf. Table, p. 387). Here are a number of closely related forms, some of which are progressively modified in many ways in correlation with burrowing habits. The parasternum in the more advanced burrowers is much more extensive than in the fully limbed surface forms. We may be quite sure that in at least the majority of such lizards the parasternum is undergoing development rather than degeneration. Slight turning back might, to be sure, occur in some cases anywhere along the line, but if we handle three species we can be sufficiently certain that at least one of these will give us the conditions we require—namely a progressively developing structure rather than a degenerating one. Now in all of the stages (represented by species of the genus *Chalcides*) which we have examined, *C. ocellatus*, *C. sepoides*, and *C. tridactylus*, and in many other limbed and limbless scincs, the posterior chevrons, supposedly the developing parts of the parasternum, are not fully or not at all connected with the ribs. This can scarcely mean anything else than that the parasternal elements arise near the mid-line NOT FROM THE SKIN but in the connective tissue immediately ventral to the Rectus superficialis at a distance from the rib-ends which they join only later. This is all we need show, after consideration of the evidence given under other headings, to demonstrate (even in the absence of direct embryological data for lizards) that the parasternum of the Sauria is similar to that of *Sphenodon*.

## (5)

In *Sphenodon*, the parasternum is bony; it is sometimes so in lizards. It lies in the superficial layer of the Rectus and beneath (dorsal to) the tendinous fascia of the Obliquus abdominis externus; it does so in lizards. It extends outward laterally beyond the rib-ends with which it



connects; it occasionally does the same in lizards. It arises separately from the ribs as a mid-ventral structure developed in the subcutaneous connective tissue (cf. Voeltzkow, 1902); it arises apparently in this manner in lizards. The parasternum in crocodiles and in *Sphenodon* is similar in all its relations except that, as in the lizards, the chevrons of the crocodile correspond to the metamerism of the body while, in *Sphenodon*, they are twice as numerous (Voeltzkow, *loc. cit.*, Daiber, 1921).

This significant difference between the condition in *Sphenodon* and in the Sauria seems to involve the question of the origin of the parasternum itself. Voeltzkow and Döderlein (1902), Williston (1916), and many others call attention to the fact that the parasternum in the more ancient fossil amphibians and reptiles is often less localized than in recent forms. In the Cotylosauria and *Theropleura* (Williston, *loc. cit.*) and *Ophiacodon* (Williston and Case), and in *Kadaliosaurus* Credner (1889), the parasternalia consist of a multitude of small bars or segments of bars, lying as a series of closely set chevrons, numbering six to each pair of true ribs. Even more numerous than this are the transverse elements of the plastron in the amphibian *Melanerpeton*. In crocodiles, dinosaurs, birds (*Archæopteryx*), Pterosaurs and lizards, on the other hand, the number of parasternal bars is reduced to one for every body segment. Howes and Swinnerton (1903) determine that each parasternal bar of *Sphenodon* arises as a number of separate fragments. These become fixed in the adult so that each chevron normally consists of three segments. We would therefore surmise that the arrangement in *Sphenodon* represents a slightly less advanced stage than in lizards and that the parasternum is tending to disappear among lizards, especially in the Anguimorpha, where neither an extreme aquatic habitus (Mosasauridæ) nor an extreme burrowing one (Anniellidæ) have succeeded in redeveloping it.

Our conclusion would be that the sternum and xiphisternum are modified parasternal structures originally represented as mid-ventral, serially homologous parasternalia quite separate from the ribs. Some embryological evidence does not support this view. Goette (1877), in lizards, and Schauinsland (1903), in *Sphenodon*, find that the sternum arises in connection with the ribs. Goette considered the sternum of the salamanders, which arises in the way we should expect on the parasternal hypothesis, to be non-homologous with the "costal sternum" of amniotes. But Rathke (1853) viewed the saurian sternum as non-costal, and Bogoljubsky (1914) has found good evidence for this in early embryos of *Lacerta* where, as in salamanders, the sternal anlage are separate from



the ribs, arising as a paired clump of cells on the mid-line and developing independently for a time.

Hanson (1919) has reviewed and added significant results which support the non-costal theory of the origin and the universal homology of the tetrapod sternum. But he goes so far as to regard the copula of the pectoral girdle in Elasmobranchs as a true sternum and presents evidence to show the common origin of the scapulo-coracoid and sternum, while considering the parasternal structures as something apart.

Most of Hanson's evidence comes from the field of mammalian embryology. His comparisons of conditions in reptiles and amphibians are largely based on adult and highly specialized forms and even these scarcely show his contention that the scapulo-coracoid and sternal apparatus are of similar origin. He does not refer to the investigations of Bogoljubsky (1914) who clearly demonstrates that in *Lacerta* the sternum arises much later than the scapulo-coracoid and quite separately from that structure.

### 23.—THE EPIPTERYGOID

The epipterygoid (columella cranii) is of interest because of its reduction or absence in burrowing forms, its reduction in some Agamidæ, and its complete absence in the chameleons.

It is totally lost in a few extreme subterraneans (Dibamidæ, Boulenger, 1887; Amphisbænidæ, Cope, 1892a). In *Anniella*, Cope denies its presence; Baur (1894) discovered it; Coe and Kunkel (1906) claim to have recognized it but do not show it in their figures.

Stannius (1856) found it absent in the chameleons. Dollo (1884) thought he had discovered it in *Chamæleon vulgaris*, but Siebenrock (1892) thinks that the bone Dollo saw was the orbitosphenoid. In a skeleton of *Chamæleon vulgaris* at hand prepared by Frič, the orbitosphenoid can be traced in its usual lacertilian position within the membrane closing the brain-case in front of the paroccipital. No trace of an epipterygoid can be seen.

In connection with the question of relationship of the chameleons to the agamids, it is noteworthy that the only limbed lizards (non-burrowers) in which the epipterygoid is greatly reduced are *Lyriocephalus*, *Phrynocephalus*, and certain other Agamidæ (Siebenrock, 1895 b).

In the Scincoidea the epipterygoid is met dorsally by a long, descending process from the parietal. A pocket in the dorsal surface of the pterygoid receives its base.



## 24.—THE PALATE

A united palate formed by contact of the pterygoids in the mid-line is found only among the Scincidæ (Boulenger, 1887) and Agamidæ where the condition is doubtless secondary. The primitive scincs *Trachysaurus*, *Tiliqua*, and *Egernia* have the pterygoids well separated. The agamids *Gonocephalus godeffroyi*, *Calotes cristatellus*, and *C. versicolor* have the pterygoids in contact (Siebenrock, 1895b). The pterygoids are separate in *Aræoscelis* (Williston, 1914).

It is interesting to note the investigations of Göppert (1903) who illustrates how closely the fleshy and bony parts of the palate reflect the shape of the tongue in lizards and in birds. Here no true secondary palate is present and the tongue serves to close the naso-pharyngeal passages during respiration. In *Varanus* and in the Serpentes where the tongue is attenuate, the floor of the mouth appears to serve the required function. In *Varanus* and possibly in the mosasaurs (cf. Baur, 1892a and Williston, 1898, Pl. XII) grooves which appear to accommodate the tongue are present anteriorly in the prevomerine bones. Accordingly the tongue in the mosasaurs must have been long and forked as in *Varanus*.

## 25.—THE PINEAL FORAMEN

The presence or absence and position of the pineal (parietal) foramen may indicate certain evolutionary tendencies. The foramen is usually pierced between the parietals but, in the Iguania and Rhiptoglossa, where these bones are constricted posteriorly it sometimes migrates forward to lie in the fronto-parietal suture (*Iguana*, *Cyclura*, *Basiliscus*, *Corythophanes*, *Xiphocercus*, *Norops*—Boulenger, 1890; most Agamidæ—Siebenrock, 1895b), or entirely within the frontal (*Dipso-saurus*—Cope, 1892a; *Sitana ponticeriana*, *Gonocephalus kuhlii*—Siebenrock, loc. cit.; *Uromastix spinipes*—Beddard, 1905b, *Chamæleon* and *Brookesia*—Siebenrock, 1893a).

There is no foramen in the recent Gekkota including *Coleonyx* and *Uroplates*; in the agamid *Liolepis belliana* (Siebenrock, 1895b); in the scincomorphs *Xantusia*, *Cnemidophorus*, *Tupinambis*, and the Amphisbænidæ; and *Voeltzkowia mira* and *Zonosaurus madagascariensis* (W. J. Schmidt, 1909). In *Cicigna* and *Cordylosaurus* (Hoffmann, 1890) the foramen is lacking. In *Gerrhosaurus* the opening is closed but a clear space is present at its former location. The foramen is also absent in many of the Diploglossa including the Pygopodidæ, *Heloderma*, †*Peltosaurus*, *Anguis*, and *Anniella*. It is very small in the Eocene glyptosaurids, *Xestops* (Fig. 103) and *Glyptosaurus*, and is present in the Jurassic gecko, *Ardeosaurus*.



W. J. Schmidt (1909) has investigated the structure of the pineal organ in many lizards and reviews most of what is known on the subject. He finds the organ reduced and the eye lacking in the Gekkota, in *Zonosaurus*, and in *Voeltzkowia mira*. The loss of the foramen is accompanied by a loss of the eye in every known case except in *Gerrhosaurus* and *Anniella* (Coe and Kunkel, 1906). In the latter the eye may "function" through the transparent parietals.

In the Iguanidæ and Agamidæ the eye is optically imperfect and lacks a nerve connection. Similarities between *Draco* and *Chamæleon* have been noted. In both the eye is extremely small and degenerate and the foramen is minute.

In the Scincidæ and Lacertidæ a nerve sometimes remains in the adult. The size of the foramen has no relation to the size of the eye in the latter group. Those who would relate functional significance of the eye with size of the foramen in fossil forms should note this.

Nowikoff (1910) believes that the eye is an organ of protection since, he claims, it is not developed in animals which are of large size, which are nocturnal, or which live out of harm's way in the tops of trees (*Draco* and *Chamæleon*). This theory is likely to be discountenanced. Experimental evidence so far is negative. Nowikoff finds the eye non-functional in the Varanidæ—the lens being filled with dark pigment.

It is suggestive that in certain Scincidæ and in *Amblyrhynchus*, where a heavy skull covering of dermal bone occurs, the foramen still persists. This may mean that the eye retains some function as an optical organ in these forms.

## 26.—THE DERMAL SCUTES

The systematic importance of the differences in structure of the bony plates underlying the horny scales in certain lizards was first appreciated by Duméril and Bocourt (1870). No satisfactory investigation of the comparative morphology and histology of these structures appeared however until the recent work of Otto (1909), the further investigations of Stehli (1910), and the extraordinary researches of W. J. Schmidt (1910, 1912, 1913, 1914, 1915).

Otto developed some interesting systematic views based almost wholly upon his idea of the evolution of the various types of structure of the bony plates and their relation to the horny scales. He considered the conditions found in geckos (cf. Fig. 83) illustrative of the most advanced stage; that of *Zonurus* (Fig. 90) the most primitive. All degrees of intermediate structure were noted between these two extremes (Figs.



84-98). His theory of the direction of evolution of the bony scales is apparently supported by conditions observed in regenerated tails of scincs and in embryonic stages of *Anguis*. In these he thought he could distinguish a more "primitive" (more *Zonurus*-like) type of scute structure and arrangement. On the basis of these observations he places *Zonurus* and *Pseudopus* (*Ophisaurus*) in a family opposite the Scincidæ and he regards the genus *Anguis* as a sort of link between the two. After an examination of the evidence we shall reconsider these views.

The bony dermal scutes found in lizards are developed just under the pigment zone in the uppermost layer of the cutis (Krauss, 1906). They arise from mesenchymatic cells and the epidermis is wholly unconcerned with their formation (Stehli). They are now known in the Scincidæ, Anelytropsidæ, Feyliniidæ, Gerrhosauridæ, Helodermatidæ, Anniellidæ, Anguidæ, Zonuridæ, and in a few geckos having been observed in *Tarentola mauritanica*, "*Platydactylus murorum*," and *Gekko verticillatus* by Cartier in 1872 (cf. Ficalbi, 1880); by Wiedersheim (1875) in *Phyllodactylus*; by Todaro in "*Ascalabotes*," and by W. J. Schmidt (1915) in *Geckolepis*.<sup>1</sup>

In *Tarentola* Otto finds very little correlation (none on some parts of the body) between the distribution of the small, regularly placed bony ossicles (Fig. 83) and the horny epidermal scales above them. Otto believes that he gets a more definite relation between the bony plates and the scales in the young stages of *Tarentola* but his illustration (Fig. 27) of this point is not convincing. Also on the regenerated tail of *Tarentola*, where we should expect to find phylogenetically the more primitive conditions, a horny scale defines a definite area of bony plates. But these differences seem so slight as not to appear significant.

Among the Scincidæ, Otto studied scales from various parts of the body in the genera *Scincus*, *Gongylus*, *Seps*, *Lygosoma*, *Mabuya*, and *Acontias*. In all these (cf. Figs. 84-87), bony plates are found beneath each scale but the peripheral limits of the bony scutes and the horny scales never exactly coincide, and the tubercles in each scute are so arranged as to form a mosaic-like structure of from two to many small parts. In the scales taken from the large plates under the jaw and in the cloacal region (Fig. 84) a "complex" condition is apparently reached approximating that found in the geckos. Great similarity exists in the form of scales from identical parts of the body in the various genera of scincs studied, and considerable differences obtain among the scales on different parts of the same body. Otto considers the "primi-

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<sup>1</sup>Osteoderms are developed only over the skull in the Lacertidæ, Xantusiidæ, Xenosauridæ, and in some Iguanidæ. In the Xenosauridæ they are minute, nodular, and on a small scale resemble those seen in *Heloderma* (Fig. 98).



tive" stages to be represented by the dorsal caudal scutes in Scincidæ "while those on the head show a more complicated form."

"These conditions must bring us to the conclusion that both in *Ascalabotes* which still have a double scale covering as well as in the Brevilingues [=Scincomorpha], there existed primitively a close relationship between the horny and bony structures."

Schmidt shows (Figs. 88-89) that the bony scaling in the ventral plates of the Gerrhosauridæ, as in the Scincidæ, does not exactly correspond to the form of the horny scales, and that a tendency to develop a mosaic pattern is present in this family as well as in the Scincidæ. Schmidt also believes that the simpler pattern found dorsally in *Gerrhosaurus* is more advanced than that of the Scincidæ. This would reverse the phylogeny of Otto. Stehli supports Otto's opinion chiefly on embryological evidence.



Fig. K. Imbricating osteoderms of the simple type. *Gerrhosaurus nigrolineatus*, dorsal scutes,  $\times 10$ , after Schmidt (1913a, Fig. G1, p. 83).

This is the most advanced stage found among scincomorphs and corresponds with the conditions seen in the Anguimorpha.

Otto finds in *Anguis* a stage still simpler than in the scincs. Here (cf. Fig. 92) the mosaic pattern of the bony scutes becomes almost completely obliterated and the relation of each scute to the overlying scale is more exact. In *Zonurus* and *Pseudopus* (Figs. 90, 91 and 93) the outline of the bony scute conforms exactly to that of the horny scale and the scute itself is a heavy solid piece without apparent pattern. This is Otto's most "primitive" stage. Exactly similar conditions are found in sculptured scutes of the North American Eocene Glyptosauridæ, tending to corroborate other evidence that these lizards are diploglossine (cf. Figs. 94-97). In *Heloderma* an exact relation of bony and horny elements is maintained although the scales are reduced to bead-like knobs. I think this shows that we are not dealing with a primitive condition in the osteodermal Diploglossa but with the maximum development of the bony derm that is known among lizards. We may well believe that the more generalized condition of geckos is primitive though we cannot prove it any more than Otto can demonstrate his own opposite contention.

Obliteration of osteoderms proceeds *pari passu* with profound subterranean life and has apparently occurred in the Dibamidæ. In the Anelytropsidæ and Anniellidæ the scutes are reduced, apparently by vacuolization (cf. Coe and Kunkel, 1904), but retain their group characteristics.



## 27.—THE SQUAMATION

As long ago as 1888 Boulenger had convinced himself "that in some cases, the aberrant scaling of the reproduced tail is a reversion to an ancestral form." Examples shown were the regenerated tails of a "Geissosaurine," teiid, *Gymnophthalmus*, in which the scaling was that hexagonal type of the "Cercosaurine" teiids rather than the normal cycloid form, and of an anguid, *Ophisaurus*, in which the scalation took the cycloid form of the related genus *Anguis* rather than the normal rhomboid type.

Werner (1896) in a study of the squamation of the regenerated tail in comparison with that of the embryo found support for Boulenger's discovery in the fact that in certain geckos having rows of larger tubercles on the tail the reproduced tail developed the uniform granular scaling found both on the embryo and in certain other geckos believed to be more primitive on account of the non-laminate condition of their toes.<sup>1</sup>

Werner's investigations indicate that the uniform granular lepidosis is the most primitive condition in the geckos. This view is held on other grounds by Sokolowsky (1899), by Barbour (1921) for the genus *Sphærodactylus*, and by W. J. Schmidt (1906–1915) who demonstrates the probability that in the few cases in which dorsal, imbricating scales have been developed in geckos (*Geckolepis*, *Teratoscincus*, *Teratolepis*, and others) such squamation is secondary, since the lizards in which it occurs are widely separated genetically and, for the most part, geographically.

Judging from Schmidt's figures and descriptions, and from specimens I have handled, the imbricate scales of geckos do not essentially differ from the imbricating scales of other ascalabotids including the Iguanidæ and Agamidæ. In all these there is a long "free-margin" and the scales "stand out" and are not so firmly anchored in the flesh as are the imbricating scales apparently of all the Autarchoglossa (cf. Figs. A–B).

We are therefore probably dealing with a most primitive type of squamation in the uniform granular covering of many Ascalabota. Whether this is ever developed secondarily in higher groups need not specially concern us. The important fact seems to be that the ventral parts in the Ascalabota possess a lepidosis consisting of either granular or very small imbricate scales and that the number of these for every

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<sup>1</sup>Tornier (1897) takes exception to Boulenger's theory on the grounds: (1) that in many lizards, i.e., Iguanidæ, Agamidæ, Zonuridæ, Lacertidæ, Gerrhosauridæ, certain Gekkonidæ (and certain Scincidæ), the scaling of the reproduced tail is normal; (2) that some geckos (*Pachydactylus*) seem to show an advanced rather than a reversional type of scaling in the outgrowing tail; (3) that the hexagonal, keeled scales of "Geissosaurine" regenerated tails are more advanced than the cycloid type which he regards as primitive. Boulenger's wording "in some cases" covers the first two objections, and Tornier, in the third count, does not explain why *Ophisaurus* should take on a "less advanced" cycloid form of scaling.



segment of the body is greater (except in *Sphærodactylus*, *Leiocephalus* and *Sceloporus magister* and probably in *Geckolepis* and *Teratoscincus*) than in the *Autarchoglossa*.

Smalian (1885) noticed that among amphisbænians the New World forms, *Amphisbæna fuliginosa* and *Anopsibæna kingii*, have two annuli corresponding to each body segment (I have found this to be the case also in *Amphisbæna alba* and *Rhineura floridana*), while in the Old World *Blanus cinereus* there is only one; and in *Trogonophis wiegmanni*, an African acrodont genus, there are two dermal segments to each rib. *Trogonophis*, however, is fundamentally different from the New World forms for each segment of the skin is innervated by a separate nerve (Rami lateralis of ventral branches of spinal nerves). May we consider the double or the single annulus as primitive?—the acrodont or the pleurodont series? Whatever may be the views as to the New World forms, it seems evident that the African *Trogonophis* is developed from a singly annulate type such as *Blanus*. The nerve distribution would show this and I believe that here we have an exception to what seems to be the usual rule of progressive skin metamerism, and increasingly close correspondence of ventral scale rows and body segmentation in the higher forms.

Stehli (1910) discovered that in certain snakes a single row of scales corresponds to one body segment, that in scincs and anguids there are two scale rows for every rib, and that in the geckos he studied there is no segmental arrangement of the scales. He came to the conclusion that among reptiles the segmental order is the original order, with the necessary corollary that the horny scales, when in correspondence with the segmentally arranged bony scutes, represent a more primitive condition than the diffused type found in geckos. He supports this conclusion with the observations of Hase who demonstrated a segmental arrangement of scales in bony fishes and ganoids. For his paleontological evidence he goes to *Aëtosaurus*, where the bony plates are, to be sure, segmentally arranged. *Aëtosaurus*, he thinks, represents the primitive condition one should expect to find among ancestral lizards. If all this is so we have genuine support for the conclusions of Otto (p. 395) in regard to the evolution of the bony scales of lizards. And we must dismiss our scheme of phylogeny and regard the serpents, zonurids, and anguids, and some limbless lizards as primitive, and the normal scincs and geckos as more advanced or more degenerate. If Stehli's evidence holds we must overrule the data of Werner, Sokolowsky, and W. J. Schmidt regarding lacerilian squamation, and we must believe with Maurer and Gegenbaur that the granular geckonid condition is degenerate.



Stehli would regard those forms having a single row to each segment as more primitive than those with two rows as he states in his conclusions (p. 795). This would involve the derivation of the normal zonurids from the degenerate *Chamæsauroidea*, the normal teiids from the worm-like *Bachia*, and many other equally startling cases.

I have counted the number of transverse scale rows on the belly, in correspondence with each body segment, in the following lizards:

Ascalabota (Approximate): *Thecadactylus rapicauda*—8; *Coleonyx variegatus*—6; *Sphærodactylus macrolepis*—2; *S. cinereus*—2; *Chalarodon madagascarensis*—12; *Iguana tuberculata*—6; *Sceloporus magister*—2–3; *Leiocephalus carinatus*—2; *Enyalius rhombifer*—4; *Chamæleon gracilis*—5.

Autarchoglossa: *Xantusia riversiana*—2; *Trachysaurus rugosus*—2; *Feylinia currori*—2; *Dibamus novæ-guinææ*—2; *Gerrhosaurus zechi*—2; *Lacerta ocellata*—2; *Tupinambis nigropunctatus*—2; *Cnemidophorus* sp.?—2; *Bachia intermedia*—1 (cf. Fig. 68); *Amphisbæna alba*—2; (*Amphisbæna fuliginosa*)—2; *Rhineura floridana*—2; (*Anopsibæna kingii*—2)<sup>1</sup>; (*Blanus cinereus*—1)<sup>1</sup>; (*Trogonophis wiegmanni*—2)<sup>1</sup>; *Varanus nuchalis*—3; *Pygopus lepidopus*—1; *Lialis burtonii*—1; *Hemiderma suspectum*—2; *Xenosaurus grandis*—2; *Gerrhonotus scincicauda*—2; *Ophiodes striatus*—2; *Anniella pulchra*—2; *Zonurus grandis*—2; *Chamæsauroidea macrolepis*—1; *Typhlops congestus*—2 (ophidian); *Diadophis* sp.?—1 (ophidian).

The facts appear to be that in the Ascalabota the scaly covering when imbricate is as figured by W. J. Schmidt (1906–1915, Pl. xxv, fig. 15) for *Geckolepis*. The scales are not so firmly anchored and have a longer free border than in the Autarchoglossa. Also that in the Ascalabota there are usually several (more than four) transverse ventral scale rows to each segment of the body, whereas, in the Autarchoglossa there are usually two and never more than three.

The best evidence seems to show that the most primitive features of the squamation of lizards are: (1) uniform granular scales on all parts of the body; (2) imbricating scales, when present, with a wide free-margin; (3) transverse rows of ventral scales not in correspondence with each pair of ribs; (4) osteoderms composed of many small, diffuse granules (cf. Figs. 82–83). All these features are represented only in the Ascalabota. The frequency of the lesser number of ventral skin segments aligns itself with the frequency of attachments of the specially

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<sup>1</sup>After Smalian (1885).



developed layers of the rectus muscle concerned with serpentiform or worm-like terrestrial locomotion.

### 27a.—The Femoral Pores

Gland-like organs, of which the femoral, preanal, inguinal and anal pores are the external orifices, appear in the following families (cf. Boulenger, 1885–1887, Werner, 1895, and Schaefer, 1902):—

Ascalabota: Gekkonidæ, Iguanidæ, Agamidæ.

Autarchoglossa: Xantusiidæ, Gerrhosauridæ, Lacertidæ, Teiidæ, Amphisbænidæ, Pygopodidæ, Zonuridæ.

They are absent in:—

Ascalabota: Uroplatidæ, Chamæleontidæ.

Autarchoglossa: (Scincimorpha) Scincoidea; (Anguimorpha) Anguidæ, Xenosauridæ, Anniellidæ, Helodermatidæ, and Varanidæ.

They occur universally only in the Xantusiidæ, Gerrhosauridæ and Zonuridæ. They are distributed among twenty-nine of the fifty-two genera of gekkonids recognized in Boulenger's Catalogue. Among the Iguanidæ they appear chiefly in the North American genera and in the Fijian *Brachylophus*, being absent in the Mascarine and South American forms except *Enyalioides*, *Ctenoblepharis*, *Liolæmus*, *Phymaturus*, *Amblyrhynchus*, and *Conolophus*.

Among the Agamidæ all the Australian genera and species except *Chelosania* possess the organs and they are present among representatives of this family elsewhere only in *Uromastix* and *Liolepis*.

The pores are present in the males in all genera of the Teiidæ except *Monoplocus*, *Callopistes*, *Leposoma*, *Loxopholis*, *Pholidobolus*, and *Macropholidus*.

All the Lacertidæ except the genus *Aporosaura* have pores in both sexes. In *Tachydromus* the pores are inguinal.

In the Amphisbænidæ the pores are represented in all genera except *Rhineura*, *Lepidosternon*, and *Trogonophis*.

The pygopodid genera *Pygopus*, *Cryptodelma*, and *Lialis* retain preanal pores. The burrowing forms *Delma*, *Pletholax*, *Aprasia*, and *Ophioseps*, lack them.

In the Autarchoglossa the pores are usually restricted to a single row. Among the Ascalabota several rows or patches may be present as in the New Zealand geckos *Naultinus* and *Hoplodactylus* (cf. Fisher, 1883, Abhandl. Naturwiss. Verèins. Bremen, VII, Pl. xvi, fig. 3). In *Thecadactylus australis*, from the islands of Torres Straits, a subtriangular patch of eighteen pores is said to occur in the males, whereas in the



American species, *rapicauda*, referred to the same genus, there are no pores.

This interesting, patch-like arrangement in the Australian and New Zealandian geckos would seem to be a primitive condition retained in these forms. The Australian and North American distribution of *Iguania* having femoral pores, together with the presence of so-called "false pores" in certain extra-Australian agamids, might lead one to suppose that secondary development in the phylogeny does not occur, but such a conclusion would scarcely be in line with what we know of the histological structure of the incipient pores of certain agamids and *Varanidæ*.

Tölg (1903) has described and figured the supposedly secondary papillæ of *Agama inermis* and *Agama stellio*, and makes it plain that these organs may be considered as true, incipient pores. That they cannot so well be regarded as vestiges follows from their occurrence on the belly of *Agama stellio*. Tölg also finds them in the inguinal region of *Varanus griseus* (cf. K. P. Schmidt, 1919, p. 488). He regards the papillæ as representing the first stages in the development of the usual, more deeply invaginated and glandular epidermal organs. He finds what he considers an intermediate stage in *Lacerta muralis* var. *maior*.

That the glands may undergo histological differentiation in some groups is indicated by the results of Cohn (1904) who discovers a very highly developed type of femoral organ in *Cnemidophorus lemniscatus*.

Félizet (1911) has shown that the glands arise in the embryo of *Lacerta* as pockets in the profound layers of the epidermis.

Duvernoy, Wagler (1830), and Johannes Müller first noted the glandular nature of the femoral organs. The histology has been investigated by Leydig (1872), Schaefer (1902), Cohn (1904), Tölg (1903), Félizet (1911), and others. Félizet remarks upon the similarities with the mammalian sebaceous gland: "La glande fémorale de l'adulte présente une évolution identique à celle de la peau ou plutôt à celle d'une glande sebacée. . . tout comme les cellules des glandes sebacées (les cellules) se rapportent à deux types." This was also partly the view of Meissner (1832), Leydig, and Schaefer, and many later workers. Tölg objects to it considering the "secretion" in the adult as the cellular modified form of the horny layer of the epidermis, a point which Félizet's observations do not seem to contradict. Tölg further states: "Wir haben es also, wenn wir die Verhältnisse nochmals überblicken, in den Femoralorganen mit scharf begrenzten Teilen der Oberhaut zu tun, die sich von dieser nur dadurch unterscheiden, dass sich hier der Ver-



hornungsprozess mit einer besonderen Intensität, aber nicht periodisch wie in der Haut abspielt, sondern einen mehr regelmässigen, stetigen Verlauf nimmt. Den Beziehungen der Femoralorgane zu einem umfangreichen lymphraum kann ich keine besondere Bedeutung beimessen."

The last sentence is in reference to the view of Maurer who believed that the proximity of lymph spaces indicated a similarity to the musk glands of crocodiles. Eggeling (1914) evidently regards the pores as paleotelic and relates them to the callous patches developed in male newts during the breeding season. Such a view appears improbable.

The glands are seemingly of functional significance and not vestigial or rudimentary structures, as might appear from their erratic distribution in some groups. In most geckos they occur only in the males. This is also true of certain teiids and of the iguanid *Phymaturus*.

Meissner (1832) studied the structures in many genera, observing that the pores were often greatly enlarged in the males. Otth (1833) confirmed this by observation of captive *Lacerta*, finding that enlargement occurred during the breeding season. Without recognizing the structure as being glandular, he regarded the pores as an accessory copulatory mechanism. It has been subsequently noted that the organs are passive in both sexes during the greater part of the year and that active secretion occurs only in the males at the time of breeding. This indicates a sexual function, the nature of which is not definitely known. Observations of Collin de Plancy (1877) and others on the mode of copulation would suggest that the waxy secretion may serve to maintain closer adhesion during the embrace.

Conclusions are that the femoral organs, functionally of some importance, are sometimes secondarily developed in the Ascalabota. Varying degrees of complexity in different forms tend to show how this might happen. Less complete localization of the pores in certain geckos may signify primitiveness of those forms; and the complete absence in certain groups and universal presence in others is of systematic interest.

## 28.—THE SHOULDER MUSCULATURE

Fürbringer (1900) in his great work on the reptilian pectoral girdle has investigated the shoulder musculature in a number of lizards. None of the systematic points he discusses seem of more significance than the variation in form of the proximal belly of the Biceps brachii (cf. pp. 421–425 and Pl. XIII, figs. 127–132).

Progressive specializations and reductions occur in this muscle which seem to be of evolutionary consequence.



The primitive condition appears to be represented in all Gekkonidæ examined, in most Scincidæ, and in a gerrhosaurid (*Hemidactylus*, *Gekko*, *Tarentola*, *Ptychozoon*, *Lygosoma*, *Gongylus*, *Zonosaurus*). In these the proximal belly is simple, undivided, and fleshy throughout.

In what Fürbringer calls the "next stage" a small tendon of origin appears alongside the proximal fleshy bundle. Such a condition obtains in the scincomorphs *Trachysaurus*, *Lacerta*, *Ameiva*, and *Tupinambis* and in the genus *Zonurus*. In *Varanus* this tendon has become enlarged and the fleshy belly reduced and directed somewhat backward. In the Iguania,—*Phrynosoma*, *Liolepis* and *Uromastix*, a division of the tendon into two or more parts occurs. Finally a total reduction of the fleshy belly appears and the biceps comes to have a long tendinous origin—*Uroplates*, *Iguana*, *Phrynosoma* (according to Rüdinger), *Stellio*, *Calotes*, *Chamæleon*, and *Heloderma* (cf. Shufeldt, 1890).

I have checked this character and find that in the primitive gecko, *Coleonyx variegatus*, the tendinous band between the two bellies of the biceps is scarcely wider than an inscription; that in *Gerrhosaurus zechi* the proximal belly is completely fleshy as in many scincoids; that the conditions in *Gerrhonotus*, *Zonurus*, and *Xenosaurus* are very similar, and different from other forms (cf. Figs. 64–65). In these three diploglossids a small tendon of origin is developed posteriorly instead of anteriorly to the fleshy proximal belly and this tendon is separate well down into the distal belly of the biceps. In the third stage along with *Liolepis*, *Uromastix*, etc., I should place *Brachylophus fasciatus* which has not completely lost the fleshy proximal bundles. My observations on *Uroplates*, *Calotes*, and *Phrynosoma* agree with those of Fürbringer.

#### 29.—THE ELEVATION OF THE SKULL

Boulenger (1920) in a monographic study of the Lacertidæ, in which the paleontology as well as the comparative structure and taxonomy is considered, outlines certain evolutionary modifications that he believes can be determined in this family. First among these tendencies are listed reduction of palatal teeth and FLATTENING and weaker ossification of the skull. Méheleÿ (1907), likewise in a review of the Lacertidæ, adopts a system diametrically opposed to that of Boulenger and regards those forms with elevated skulls as derived from the flat-skulled types. To do this, however, Méheleÿ is forced to obtain palatal teeth from absence of teeth, parietal foramina from forms in which these do not exist, normal eyelids from genera in which a transparent disc has been developed, non-denticulate from denticulate ear-openings, normal digits



from digits elongate and compressed, nostrils pierced in the center of the nasal from nostrils enclosed between two or more plates, and striated from spotted types of coloration (in opposition to the views of Eimer, Cope, and Gadow as to the origin and history of the color pattern in the Lacertoidea. (Cf. Boulenger, *loc. cit.*)

In the Lacertidæ at least we choose to conclude with Boulenger that the elevated type of skull is primitive. It is probable that this also holds true in the Scincidæ where certain Australian forms, in certain other respects primitive (*Trachysaurus*), have a relatively elevated type of skull. In *Trachysaurus* the inner (orbital) angle of the jugal approaches 90°. In the anguimorph Eocene family, the Glyptosauridæ, this is also the case (cf. Douglass, 1908, p. 278, Fig. 2; also Figs. 103, 106, 107 of the present paper).

The elevated skull is possibly developed secondarily in some Iguania and in the Rhiptoglossa (cf. *Amblyrhynchus*, *Uromastix*, and some other agamids, and the chameleons).

### 30.—THE OS HYPOISCHIUM

A cartilaginous or calcareous os hypoischium occurs as far as known in all genera of limbed lizards except certain geckos, the Xantusiidæ, a single iguanid *Chalarodon*, most Scincidæ, and the Rhiptoglossa. I have found it absent in cleared or alcoholic specimens of the following: *Hemidactylus*, *Phyllodactylus*, *Lepidoblepharis barbouri*, *Coleonyx variegatus*, *Lathrogecko xanthostigma*, *Gonatodes annularis*, *Chalarodon madagascarensis*, *Xantusia vigilis*, *X. riversiana*, *Chamæleon vulgaris*, *C. dilepis*, *Egernia cunninghami*, *Dopasia smaragdinum*, and *Plestiodon quinquelineatus*. Siebenrock (1893b) has noted its absence in *Brookesia* and *Chamæleon*, and states it to be universally absent in the Scincidæ.

Gadow (1882b) has failed to find the bone in *Phrynosoma cornutum* but it is present in all western species of *Phrynosoma* according to Bryant (1911).

The element has been seen in the following genera. Where no authority is cited, I am responsible for the examination.

Gekkonidæ: *Sphærodactylus macrolepis* (Noble, 1921, p. 11, Fig. 6B, "rudimentary or wanting"), *Coleonyx variegatus* (Noble, *loc. cit.*), *Pachydactylus maculatus* (idem, "extremely long"). *Thecadactylus*, *Gehyra*, *Phyllodactylus*, and *Gekko verticillatus*, *Gekko* (Mehnert, 1891), *Platydictylus mauritanicus* (Ficalbi, 1880).

Uroplatidæ: *Uroplates fimbriatus* (Siebenrock, 1893b,—the bone is triangular in shape and extends farther posteriorly, in a specimen at hand, than Siebenrock has figured it).



Iguanidæ: *Holbrookia maculata approximans*, *Crotaphytus collaris baileyi* (both ♂ and ♀, but stronger in the ♂), *Iguana tuberculata* (Hoffman, 1890), *Iguana delicatissima* (Gadow, 1882b), *Amblyrhynchus cristatus*, *Brachylophus fasciatus*, *Sauromalus hispidus*, *Basiliscus amboinensis* (Hoffmann, loc. cit.), *Polychrus marmoratus* (idem), *Anolis sagræ*, *Norops auratus*, *Xiphocercus heterodermus*.

Agamidæ: *Japalura swinhonis*, *Agama plica* (Hoffmann, 1890), *Gonocephalus subcristatus* (Mehnert, 1891), *Liolepis guttata* (idem), *Calotes versicolor*, *Draco formosus*; and in the following listed by Siebenrock (1895b): *Charasia*, *Phrynocephalus*, *Amphibolurus*, *Lophura*, *Uromastix*, *Moloch*, *Sitana*, *Lyriocephalus kuhlii*, and *Acanthosaura*.

Scincidæ: *Trachysaurus rugosus*, absent in *Tiliqua* according to Werber, 1865.

Gerrhosauridæ: *Gerrhosaurus*.

Lacertidæ: All forms examined by Siebenrock (1894) including *Lacerta*, *Algiroides*, and *Acanthodactylus* (cf. also Mehnert, 1891).

Teiidæ: *Ameiva surinamensis* (Mehnert, 1891), *Ameiva vulgaris* (Gadow, 1882b), *Tupinambis nigropunctatus*.

Varanidæ: *Varanus niloticus*, *V. exanthematicus*, *V. nuchalis*, *V. bivittatus* (Hoffmann, 1890), *V. salvator* (Mehnert, 1891).

Pygopodidæ: *Pygopus lepidopus* (Cope, 1894b, Pl. XIII, fig. 3b and c, [=Hypogastroid].) The cartilage is totally divided, one half attaching to each of the widely separated halves of the ischio-pubis. If we knew the ontogeny of this interesting condition it might be found to support Mehnert's conception of the paired origin of the hypoischial cartilages.

Helodermatidæ: *Heloderma suspectum*.

Xenosauridæ: *Xenosaurus grandis*.

Anguidæ: *Gerrhonotus scincicauda webbiai*, *G. imbricatus* (Siebenrock, 1895a), *Ophiodes striatus* (Fürbringer, 1869—here, with separation of the much reduced ischii the symphysis has been lost but the Y-formed "Cartilago cloacalis" still remains joined to each ischium in the usual way. Cf. also Cope, 1892b, Pl. XIII, fig. 2b).

Zonuridæ: *Zonurus giganteus*, *Chamæsauro macrolepis* (Cope, 1894b, Pl. XIII, fig. 1b—very large in comparison with rest of pelvis and apparently degenerating at a slower rate.)

The shape is usually elongate and pointed (Fig. L1), often with a split at the distal extremity (Fig. L2) where the tips curve around the insertions of the Mm. Transversus perinei, and sometimes (Fig. L3) arising from each ischium. Rarely is the bone short and rectangular (Fig. L4) (cf. *Uroplates*).



The os hypoischium, discovered in *Phrynosoma* by Spring and Lacordaire (1842), has been studied by Mehnert (1891) and Wiedersheim (1872) in connection with other pelvic median elements at one time supposed to represent the phylogenetically oldest portion of the girdle. The late appearance of the os hypoischium, derived, according to Mehnert, from the ischium, and of the os epipubis which arises from the pubis in a similar manner, would seem to discredit the view that these elements represent primitive parts present in *Protopterus*. It is also claimed that no developmental relation exists between the ligamentum medianum (symphyseal ligament) and the end bones, epipubis and hypoischium. The ligamentum medianum develops as a muscular septum and later obtains a secondary pelvic connection.

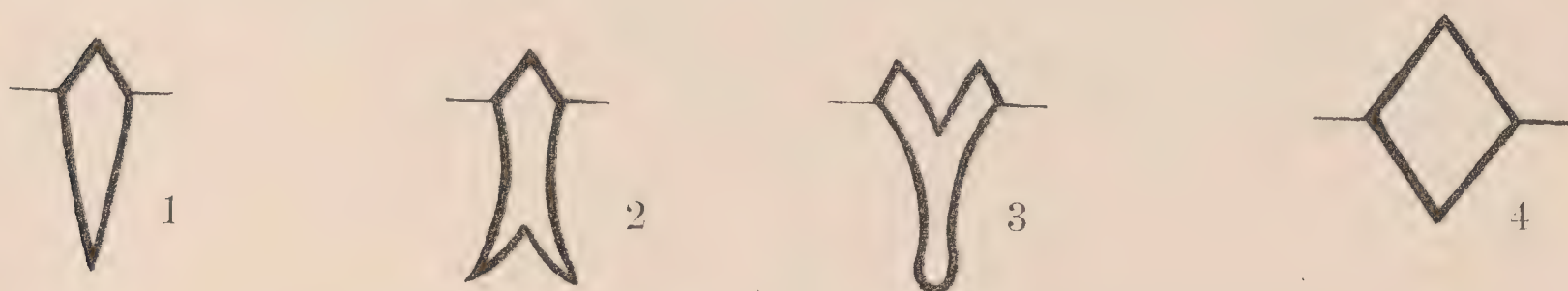


Fig. L. Various types of the os hypoischium.

In adult material the hypoischium has every appearance of being a posterior continuation of the symphysial ligament but according to Mehnert the whole hypoischial structure (os hypoischium and ligamentum hypoischium) is a direct outgrowth of the median posterior portion of the primordial ischial cartilage.

Mehnert's figures (Pl. VIII, figs. 3 and 4) do not clearly show all points of his contention. It would appear very probable that the so-called perichondrial tissue of the developing cartilaginous anlage of ischium and hypoischium (Fig. 4) is represented by the medial so-called hypoischium of an earlier stage (Fig. 3) and that the origin of this tissue may well be the medial ends of the ischii (Fig. 2). There really appears to be no embryological ground for the statement that the os hypoischium originates in two parts since, as Mehnert admits and illustrates (Fig. 4), the center of ossification arises in the perichondrial tissue as a single cartilaginous element separate from the ischii. It never becomes a true bone in lizards, and its distribution might better be accounted for on the view that the element is only an epiphysial calcareous deposition in the ligamentum hypoischium than that we are dealing with a more primitive degenerating element as Mehnert would suggest. This lessens the paleontologic value of the structure and prevents us from regarding the



distribution in *Menobanchus* and *Didelphys* as indicative of primitiveness, or as offering homology with the lizard bone.

The ligamentum hypoischium, universally present in limbed lizards, lies between the median termini of the large transverse perineal muscles which constrict the base of the tail. A chondrification or calcification frequently occurs in this ligament and may extend along the entire ligamentum medianum as far as the pubis (cf. Wiedersheim, 1892; also Bryant, 1911, Figs. A and B, and Siebenrock, 1895*b*, Figs. 32, 34, 38). There is often a suture or foramen at the basal end of the hypoischial bone which would indicate a separate center of calcification for the os hypoischium as Mehnert has found.

The os hypoischium is absent in *Sphenodon*, and also, so far as known, in the extinct reptilia and amphibia. It is apparently a neomorph in lizards; develops early in the phylogeny; is not represented in most primitive geckos though occasionally developed in that family; is absent in the relatively primitive xantusids and in most scincids and possibly has been lost in *Chamæleon* owing to reduction of the Mm. Transversus perinei.

The Varanidæ alone among lizards is the anterior representative of the os hypoischium, the epipubic bone, paired.

### 31.—THE PATELLAR SESAMOIDS

The patella ulnaris lies in the tendon of insertion of the triceps which rides over the end of the humerus to reach the olecranon. It is partly bony in most of the Ascalabota and cartilaginous in most Autarchoglossa. When cartilaginous it merges insensibly into the fibers of the triceps tendon. It would seem possible that its weaker development in the latter group is associated with use of the belly muscles for purposes of locomotion. Unfortunately, for this theory, however, the element is bony in the scincs, *Tiliqua* and *Trachysaurus*, (cartilaginous in *Egernia*), and in *Tupinambis*.

Fürbringer (1900, pp. 443–444, 459, Pl. xv, figs. 147–158) is not inclined to regard its form and distribution as of great significance in lizards. He found the patella ulnaris in all the forms he examined, it being bony or partially so in the ascalabotids, *Hemidactylus*, *Gekko*, *Ptychozoon*, *Uroplates*, *Phrynosoma*, and *Calotes*,—and in *Lacerta*; and cartilaginous (faserknorpelige) in the autarchoglossids, *Lygosoma*, *Zonosaurus*, *Zonurus*, *Ameiva*, and *Varanus*,—and in *Chamæleon* and *Brookesia*.



Cope (1892a) has found the patella tibialis only in *Varanus*. It is also present and bony in *Tiliqua*, *Trachysaurus*, and *Gerrhosaurus*, and I have seen it bony in no other forms. It seems to be neomorphic and the ulnar patella is doubtless of like nature in the bony state.

A peculiar bony fibular interarticular sesamoid is sometimes developed in the internal femero-fibular ligament lying beneath the broad insertion tendon of the Rectus femoris in which the patella tibialis develops. This element is present in *Crotaphytus*, *Sauromalus*, *Iguana*, *Cyclura*, *Chamæleon vulgaris*, *Egernia*, *Trachysaurus*, *Tiliqua*, *Gerrhosaurus*, and *Tupinambis*. It is double in *Egernia*. It seems to be present, along with a bony patella, in the dolichosaur *Opetiosaurus* (Nopcsa, 1903). Banchi (1900) has named this bone the parafibula. He finds it in *Lacerta ocellata*, *Varanus arenarius*, *Chamæleon vulgaris*, *Platydictylus mauritanicus* and *Gongylus ocellatus*. He regards it as a primitive element, the remnant of a third metapodial, because of its large size and separate development in the embryo.

### 32.—THE STERNAL FONTANELLES

Sternal fenestræ are present in most of the families of lizards exclusive of the Anguimorpha, where they have never been found. A single fontanelle occurs in most Iguanidæ, most Scincoidea, and Lacer-toidea, and in the amphisbænoid *Chirotes*. *Xantusia vigilis* has a very small double fenestra (cf. Fig. 69). In a few Iguanidæ the opening is divided by a median strip of cartilage and in all known Agamidæ having a perforate sternum, the fontanelles are double.

In the following synopsis the capital letters in parentheses refer to Cope (1892), and Siebenrock (various papers).

#### NO FONTANELLES:—

Gekkota: *Phyllodactylus tuberculatus* (C), *Gonatodes atricucullaris* (Noble, 1921), *Paragonatodes dickersoni* (idem), *Lepidoblepharis barbouri* (idem), *Platydictylus guttatus* (Calori, 1861), *Hemidactylus ovalensis* (Gegenbaur, 1865), *Gonatodes annularis*, *Gehyra*, *Lathrogecko xanthostigma*, *Coleonyx variegatus*, *Uroplates fimbriatus* (S).

Iguania: *Læmanctus longipes* (Parker, 1868), *Chalarodon madagascarensis*, *Sauromalus* (C), *Crotaphytus wislizenii* (C), *Polychrus* (C), *Lyriocephalus* (Boulenger 1885), *Lophura* (S), *Moloch* (Boulenger, 1885, states that the sternum has a longitudinal median suture. In specimens examined by Siebenrock, 1895, this was not observed).

Anguimorpha: *Gerrhonotus multicarinatus* (C), *Gerrhonotus scincicauda*, *Anguis fragilis* (C), *Ophisaurus ventralis* (C), *Dopasia gracilis*



(C), *Ophiodes striatus* (C), *Xenosaurus grandis*, *Heloderma suspectum* (Shufeldt, 1890), *Delma fraseri* (Müller, 1900), *Pygopus lepidopus* (C), *Varanus bengalensis* (Parker, 1868), *Tylosaurus dyspelor* (Osborn, 1899), *Clidastes dispar* (Fürbringer, 1900, after Marsh), *Zonurus cordylus* (Fürbringer, 1900), *Chamæsaura macrolepis* (C).

Rhoptoglossa: *Brookesia* (S), *Chamæleon quilensis* (Methuen and Hewitt, 1914), *C. demaranus* (idem), *C. ventralis* (idem), *C. brevicornis* (idem), *C. lateralis* (idem), *C. dilepis* (idem), *C. vulgaris* (Gegenbaur, 1865), *C. gracilis*.

Scincomorpha: *Plestiodon aldrovandi* (Gegenbaur, 1865), *Trachysaurus rugosus* (idem), *Mabuya multifasciata* (S), *Gongylus ocellatus* (Müller, 1900), *Chalcides lineatus* (C), *Evesia monodactyla* (C), *Tiliqua nigrolutea* (Parker, 1868), *Egernia*, *Zonosaurus ornatus* (S), *Propus vermiformis* (C), *Blanus cinereus* (Müller, 1900).

#### A SINGLE MEDIAN FONTANELLE:—

Iguanidæ: *Phrynosoma* (many species, Bryant, 1911), *Iguana tuberculata* (Parker, 1868), *Anolis carolinensis* (C), *A. sagræ*, *Dipsosaurus dorsalis* (C), *Crotaphytus collaris* (C), *Sceloporus undulatus* (C), *S. spinosus* (C).

Scincomorpha: *Eumeces obsoletus* (C), *E. fasciatus* (C), *Lygosoma quoyi* (S), *L. tæniolatus* (S), *L. sundevallii* (S), *Mabuya striata* (S), *Chalcides mionecton* (S), *Gerrhosaurus nigrolineatus* (S), *Lacerta agilis* (Gegenbaur, 1865), *L. simonyi* (S), *L. muralis* (S), *L. oxycephala* (S), *L. mosorensis* (S), *Ophiops* (S), *Acanthodactylus* (S), *Eremias* (S), *Cnemidophorus tessellatus* (C), *C. sexlineatus* (C), *Bachia intermedia*, *Chirotes canaliculatus* (Parker, 1868).

#### TWO FONTANELLES:—

Iguanidæ: Some species of *Holbrookia* (specimens prepared by Miss M. C. Dickerson and described by her in MS.).

Agamidæ: *Gonocephalus kuhlii* (S), *Agama atra* (S), *Liolepis beliana* (S), *Grammatophora barbata* (Gegenbaur, 1865), *Agama stellio* (Calori, 1859b), *Physignathus lesueurii* (Beddard, 1905b). *Calotes jubatus* (Boulenger, 1912), *Calotes versicolor*.

Scincimorpha: *Xantusia vigilis*, *Ablepharus pannonicus* (S. Here there is a small anterior and a larger posterior fontanelle, the latter being partially divided), *Lacerta muralis* var. *cærulea* (S).

Siebenrock (1895b) finds the sternal fontanelles much larger in the young of certain agamids. He explains this on the assumption that the fontanelles are formed directly by incomplete union of the two halves



of the embryonic sternum, basing this idea on Goette's observations (1877). Bogoljubsky (1914), however, has shown that the openings arise by resorption of the mesenchymatous and cartilaginous median parts after complete union of the sternal halves. It seems probable that the fontanelles are sometimes of secondary development, possibly in connection with certain relations of the Pectoralis musculature. Their non-appearance in the Anguimorpha and rather uniform distribution in some other groups give them a systematic value.

### 33.—THE SCAPULO-CORACOID FENESTRÆ

Fenestræ are present in the coracoid and anteriorly between the coracoid and scapula in most lizards. Usually these are enclosed anteriorly by the cartilaginous coracoidal and scapular borders<sup>1</sup>; sometimes they are simply open emarginations. A membranous window usually closes each fenestra (cf. Figs. 64–69).

The most lateral of these openings, lying entirely within the scapula, occurs notably in the Iguanidæ and Scincidæ. Its presence results in the formation of the proscapular process, present in the Gekkonidæ and Iguanidæ, in the agamid *Lophura*, in many Scincidæ, in the teiids, *Cnemidophorus* and *Ameiva*, and in the anguid *Celestus striatus* (cf. Cope, 1892a).

The scapulo-coracoid fenestra is almost universal among fully limbed lizards but is represented in *Heloderma*, some varanoids, the mosasaurs, and a few other forms simply by an emargination and is absent in *Uroplates* and *Chamæleon*.

The first, and most lateral, coracoidal fenestra is also widely distributed, being absent so far as known only in *Heloderma*, some dolichosaurs and mosasaurs, and *Chamæleon* among the limbed forms. The second, and most medial, fenestra is irregularly distributed as indicated in the following table where X indicates the presence of a closed fenestra and E of an emargination.

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<sup>1</sup>The so-called "epicoracoids" and suprascapula of lizards are remains of the cartilaginous embryonic scapulo-coracoidal plate (cf. Goette, 1877, and Broom, 1906). The anterior coracoid (=epicoracoid or procoracoid) of theromorphous reptiles (=epicoracoid of *Ornithorhynchus*) is not to be confused with the "epicoracoid" of lizards. The bony coracoid of lizards, *Sphenodon*, and the cotylosaur, *Seymouria*, may represent both anterior and posterior coracoidal elements of theromorphs.



GEKKOTA

- Platydictylus muralis* (Calori, 1859a)
- Platydictylus mauritanicus* (Ficalbi, 1880)
- Hemidactylus oualensis* (Gegenbaur, 1865)
- Gekko verticillatus* (Boulenger, 1912)
- Gonatodes atricucullaris* (Noble, 1921)
- Paragonatodes dickersoni* (idem)
- Lepidoblepharis barbouri* (idem)
- Sphærodactylus macrolepis* (idem)

IGUANIA

- Chalarodon madagascarensis*
- Iguana tuberculata* (Parker, 1868)
- Læmanctus longipes* (idem)
- Sauromalus hispidus*
- Sauromalus varius?*
- Cyclura*
- Crotaphytus collaris*
- Crotaphytus wislizenii*
- Grammatophora barbata* (Gegenbaur, 1865)
- Stellio cordylinus* (Parker, 1868)
- Liolepis belliana* (Siebenrock, 1895b)
- Agama atra* (idem)
- Gonocephalus kuhlii* (idem)
- Lyriocephalus scutatus* (idem)
- Lophura* (Salverda, cited by idem)
- Moloch horridus* (idem)
- Calotes versicolor*
- Calotes jubatus* (Boulenger, 1912)

RHIPTOGLOSSA

- Brookesia superciliaris* (Siebenrock, 1893a)
- Chamæleon vulgaris* (Gegenbaur, 1865)
- Chamæleon gracilis*

SCINCOMORPHA

- Xantusia vigilis*
- Trachysaurus rugosus* (Gegenbaur, 1865)
- Plestiodon aldrovandi* (idem)
- Cyclodus [Tiliqua] nigrolineatus* (Parker, 1868)
- Egernia whitei* (Siebenrock, 1895a)
- Mabuia multifasciata* (idem)
- Mabuia striata* (idem)
- Lygosoma moco* (idem)
- Lygosoma ornatum* (idem)

| SCAPULAR       | SCAP.-CORACOID | 1" CORACOID | 2" CORACOID |
|----------------|----------------|-------------|-------------|
| E?             | X              | X           | X           |
| E              | X              | X           | X           |
| X              | X              | X           | X           |
| ?              | X              | X           | X           |
| E              | X              | X           | O           |
| E              | X              | X           | X           |
| E              | X              | X           | O           |
| E              | X              | X           | O           |
| X              | X              | X           | O           |
| X              | X              | X           | X           |
| X              | X              | X           | X           |
| O              | E              | X           | O           |
| X              | X              | X           | X           |
| X              | X              | X           | X           |
| X              | X              | X           | X           |
| O              | X              | X           | O           |
| O              | E              | X           | O           |
| O              | X              | X           | O           |
| O              | X              | X           | O           |
| O              | X              | X           | X           |
| O              | E              | X           | O           |
| X              | X              | X           | ?           |
| O              | E              | X           | O           |
| O              | X              | X           | O           |
| O              | X              | X           | O           |
| O              | E?             | O           | O           |
| O              | O              | O           | O           |
| O              | O              | O           | O           |
| O              | X              | X           | O           |
| X <sup>1</sup> | X              | X           | X           |
| O              | X              | X           | O           |
| X              | X              | X           | O           |
| X              | X              | X           | O           |
| X              | X              | X           | O           |
| X              | X              | X           | O           |
| X              | X              | X           | O           |

<sup>1</sup>This occurs only on the right side in one of our specimens and is absent in Parker's figure (1868).



|                                                   | SCAPULAR | SCAP.-CORACOID | 1" CORACOID    | 2" CORACOID |
|---------------------------------------------------|----------|----------------|----------------|-------------|
| SCINCOMORPHA (continued)                          |          |                |                |             |
| <i>Lygosoma smithii</i> (idem)                    | X        | X              | X              | O           |
| <i>Albepharus pannonicus</i> (idem)               | X        | X              | X              | O           |
| <i>Chalcides mionecton</i> (idem)                 | O        | X              | X              | X           |
| <i>Chalcides tridactylus</i> (Krieg, 1919)        | O        | X              | X              | O           |
| <i>Zonosaurus ornatus</i> (Siebenrock, 1895a)     | O        | X              | X              | O           |
| <i>Gerrhosaurus flavigularis nigrolineatus</i>    | O        | X              | X              | O           |
| <i>Lacerta agilis</i> (Gegenbaur, 1865)           | O        | E              | X              | O           |
| <i>Lacerta simonyi</i> (Siebenrock, 1894)         | O        | E              | X              | O           |
| <i>Lacerta serpa</i> Krieg, 1919)                 | O        | E              | X              | O           |
| <i>Lacerta viridis</i> (Calori, 1859a)            | O        | E              | X              | O           |
| <i>Tupinambis nigropunctatus</i>                  | O        | X              | X              | X           |
| <i>Bachia intermedia</i>                          | O        | X              | X              | X           |
| <i>Chirotetes canaliculatus</i>                   | O        | O              | O              | O           |
| ANGUIMORPHA                                       |          |                |                |             |
| <i>Carsosaurus</i> (Nopcsa, 1903)                 | O        | E              | X              | X           |
| <i>Dolichosaurus</i> (Nopcsa, 1908)               | O        | E              | O              | O           |
| <i>Plioplatecarpus marshii</i> (Dollo, 1882)      | O        | E              | X              | O           |
| <i>Platecarpus coryphæus</i> (Williston, 1892)    | O        | E              | X              | O           |
| <i>Platecarpus ictericus</i> (idem)               | O        | E              | X              | O           |
| <i>Clidastes velox</i> (idem)                     | O        | E              | X              | O           |
| <i>Clidastes westii</i> (idem)                    | O        | E              | O              | O           |
| <i>Tylosaurus dyspelor</i> (idem)                 | O        | E              | O <sup>1</sup> | O           |
| <i>Psammosaurus scincus</i> (Parker, 1868)        | O        | E              | X              | X           |
| <i>Monitor dracæna</i> (Parker, 1868)             | O        | X              | X              | X           |
| <i>Varanus niloticus</i>                          | O        | X              | X              | X           |
| <i>Varanus griseus</i> (Boulenger, 1912)          | O        | E              | X              | X           |
| <i>Heloderma suspectum</i>                        | O        | E              | O              | O           |
| <i>Xenosaurus grandis</i>                         | O        | X              | X              | O           |
| <i>Gerrhonotus imbricatus</i> (Siebenrock, 1895a) | O        | X              | X              | O           |
| <i>Anguis fragilis</i> (Goette, 1877)             | O        | X              | X              | O           |
| <i>Zonurus griseus</i> (Sauvage, 1872)            | O        | X <sup>2</sup> | X <sup>2</sup> | O           |
| <i>Zonurus giganteus</i>                          | O        | X              | X              | O           |

The almost universal presence of the scapulo-coracoid fenestra is suggestive of a paleotelic nature. Fürbringer (1900) is even led to think that the parts are comparable with those found in the salamanders. This view has some support from the embryological side. Bogoljubsky (1914) finds that, in the Lacertidæ and especially in the Gekkonidæ, the scapulo-coracoid and chief coracoid fenestræ develop very early,

<sup>1</sup>A trace of a lateral coracoid fenestra is present (cf. Osborn, 1899).  
<sup>2</sup>United in adult, separate in embryo (cf. *Ophisaurus*, Sauvage, 1878).



even before the sternum joins the ribs. This does not confirm the results of Goette (1877) who thought he found the early stages in *Cnemidophorus* to be "*Sphenodon*-like," nor does it agree with what we know of the fossil record. The Permian *Aræoscelis*, a supposed ancestor of the Sauria, appears to have had an unfenestrated scapulo-coracoid. Broom (1906) believes that the lacertilian girdle is "merely a highly specialized modification of the *Sphenodon* type."

The relations of the two chief fenestræ to the Supracoracoideus and Scapulohumeralis anterior muscles is illustrated in Fig. 67.

### 34.—THE ENDOLYMPHATIC GLANDS

Endolymphatic glands (Aquæductus vestibuli, Wiedersheim, 1876), extending posteriorly beyond the limits of the skull, are known in many Ascalabota including most of the Gekkota and the iguanid *Anolis sagræ* (A. M. N. H.). They are also found in *Xantusia vigilis* (A. M. N. H.), their phylogenetic importance lying in the fact that they are, so far as known, present only in this one family of the Autarchoglossa; a circumstance that strengthens evidence, from the vertebræ and hyoid, of the primitive nature of the Xantusiidæ and their more than superficial affiliation with the Ascalabota. (Cf. Fig. 43).

Ruth (1918) has given a plausible reason for the sporadic and variable occurrence of the glands. He finds an increased functional activity in certain Philippine geckos during pregnancy and especially at the time when the egg-shell is forming. After the eggs are laid the gland is exhausted and one conclusion is that the calcium secreted is poured into the blood stream to furnish material for the calcareous shells of the eggs. It is thought that a more usual function in amphibians and reptiles is to provide for growth of bone, while the original use would seem to have been to supply the calcareous otoliths of the equilibrating system.

The secretion of the glands crystalizes as Aragonite according to Physalix, but in geckos Ruth has shown it to be amorphous until exposed to the air (cf. Calori, 1861).

### DISCUSSION

The systematic arrangement should be a carefully considered compromise between the differences as they exist in living forms and the distance of phylogenetic separation of the groups. The arrangement subserves convenience to some extent and cannot express all the relationships.



There is a constant tendency for multiplication of super-groups on the basis of great morphological differences and wide separation of living forms. For the sake of "consistency" in respect to morphological, and too often cænotelic, differences, species are raised to genera, genera to families, superfamilies to suborders, until finally classification will almost cease to express relationship as indicated by paleotelic evidence.

The true phylogeny is based not upon cænotelic differences, however great, but strictly upon the distribution of related conservative features such as primitive and vestigial structures, tendencies for certain types of modification to occur, similar ontogenies, and the paleontological record.

If, for the sake of "consistency" in respect to morphological divergence, we should place the pygopodids into a separate "gens" as Fürbringer has done, we should, to be "consistent," elevate the Anniellidæ, the Feyliniidæ, and the Dibamidæ.

If we should elevate the Chamæleontidæ, we should do the same with the Uroplatidæ which have evolved along the same lines, and with the Amphisbænidæ which have gone as far in a different direction. Instead of recognizing the number of larger groups of equal rank outlined by Furbringer (1900) I have tried to arrange a system more illustrative of the phylogeny and have ventured to consider the lizards as divided into two main branches differing in lepidosis, in muscular, hemipenial, possibly in visceral, characters (cf. Cope, 1900, p. 450), and in the frequency of appearance of different tendencies of development in each line of descent. The origin of these groups seems to have been concerned with an early divergent habitus involving adaptive capabilities rather closely circumscribed by the respective morphological equipment. This equipment appears in the Ascalabota to have been perfected along lines connected with the requirements for arboreal life habits, and in the Autarchoglossa to have improved in correlation with terrestrial conditions of habitat. It seems that long association and accommodation of organism to habitat has resulted in adjustments so balanced in each group that tendencies for the more profound secondary modifications, arising in connection with arboreal life in the Ascalabota, never appear in the terrestrial group (Autarchoglossa) even among those genera which are exclusively arboreal in habit. Whereas, in the Ascalabota, profound secondary modifications for terrestrial life never occur even among the many forms which are highly terrestrial (cf. Cope, 1900, p. 201). Only the Autarchoglossa are able to fulfill the morphological requirements for advanced subterranean life although opportunities for



such development must always be gratuitously open to the terrestrial, temporarily burrowing Ascalabota. Only the latter group has been able to accept the opportunities afforded at the top of the scale of arboreal requirements, although for the arboreal Autarchoglossa such situations must be continually at hand.

In accordance with the evidence it seems that certain descent lines may carry tendencies to change in ways in which a neighboring series of forms cannot be modified. It would appear that identical characters do often "crop out" separately in one stock and that a related group may be wholly incapable of such deviation. The incapacity of geckos, iguanians, and chameleons to develop burrowing, limbless, terrestrial forms seems to be due to lack of a certain important ventral locomotory muscle, the Rectus superficialis, developed in the scincs, lacertids, teiids, anguids, and all other members of the Autarchoglossa, many of which have limbless representatives. In the latter group, mutations involving reduction of limbs may become favorable for existence of the animal in an unoccupied habitat. In the Ascalabota such mutations would leave the creature without effective means of locomotion.

## RÉSUMÉ

### SUMMARY OF CLASSIFICATION

It is proposed to divide the Sauria into two main groups, the Ascalabota and Autarchoglossa. The first of these includes the geckos, iguanids, agamids, and chameleons.

The geckos are considered as primitive, chiefly on account of the persistence of chorda in their vertebræ, the universal presence of dorso-lumbar intercentra, and the occasional complete or nearly complete third branchial arch.

The iguanids and agamids are related to the geckos on characters of the hemipenes, musculature, and squamation. *Holbrookia* and other North American iguanids are regarded as primitive, *Iguana*, *Cyclura*, *Sauromalus*, *Dipsosaurus*, and *Amblyrhynchus* as central, and *Basiliscus* and *Anolis* as offshoots of the latter group on the characters of throat musculature, number of cervical ribs, presence of femoral pores, and dentition. *Chalarodon* of Madagascar is an iguanid as shown by the dentition, throat musculature, and presence of a proscapular process. The Fijian *Brachylophus* is closely related to *Ctenosaura* and *Cyclura* on the basis of details of the throat musculature, and number of abdominal parasterna. *Liolepis* and *Uromastix* are considered primitive agamids in respect to throat musculature, structure of interclavicle,



and presence of a *Rectus superficialis* muscle. *Agama*, *Physignathus*, and *Amphibolurus* are central and *Calotes*, *Japalura*, and *Draco* derived from them. Some characters of the Agamidæ are more primitive than those of iguanids, but the dentition and frequent absence and reduction of skeletal and muscular parts place them on a higher level than the Iguanidæ.

The chameleons are offshoots of agamid stock.

The family Xantusiidæ is intermediate between the first group (Ascalabota) and the second (Autarchoglossa). The trunk vertebræ still retain an intercentrum and are of geckonoid shape; the third branchial arch is nearly complete. Skull characters, the presence of a *Rectus lateralis* muscle, and the exact relation of the ventral scales to the body segments relate the group most closely to the scincs, teiids, and especially to the lacertids. The interclavicle of *Xantusia* is cruciform and dermal skull ossifications are present.

The Xantusiidæ, Scincoidea, and Lacertoidea, with the possible inclusion of the Amphisbænidæ, form a separate group, Scincomorpha, distinct from the Anguimorpha, the latter comprising the Platynota, anguioids, and zonurids. The differences between these two groups concern the structure and relations of the ventral osteoderms, the greater complexity of the throat musculature in Anguimorpha, the texture of the tongue and hemipenes, as well as tendencies in the evolution of tooth replacement, the place of attachment of the caudal chevrons and the failure of a parasternum in the degenerate forms.

Degenerate Scincomorpha tend to develop a burrowing habitus recognized in the anatomical features; short tail, closed eyes, and ears, degeneration of limb girdles, enormous increase in complexity of body musculature, increase in the *Cervicomandibularis* muscle, increased parasternum, inflation of cranium; final loss of skull arches, interorbital septum, epipterygoids, caudal chevrons, and osteoderms.

Degenerate Anguimorpha are frequently surface-living, apparently grass-inhabiting forms which greatly increase the tail, retain the skull arches and other cranial elements, retain a more simple body musculature complete girdles, osteoderms, and functional eyes.

Further indication of the scincomorph relationship of the amphisbænians is found in the teioid form of the hyoid of the embryo of *Amphisbæna*. No special relationship with degenerate teiids or other degenerate lizards or with serpents can be expected, although the body musculature parallels that of the burrowing snakes, Typhlopidae. The throat musculature is unique but nearest that of *Varanus*.



The Mosasauroida are regarded as derived from varanoid stock through the Aigialosauridæ. The Dolichosauridæ, on account of the great number of their cervical vertebræ, reduction of limbs, and elongation of body, are believed to be a side branch and not ancestral.

The Platynota are related to the Diploglossa in hemipenial and dental characters, the ligamentary, symphyseal attachment of the lower jaws, formula of the scapulo-coracoid fenestræ, attachment of the caudal chevrons, structure of the skull arches, and lack of femoral pores.

The Pygopodoidea are considered as diploglossids rather than geckonids because of tongue texture, relation of ventral scaling to body segmentation, presence of a Rectus superficialis muscle, nondeciduate, imbricating scales and the relations of the os hypoischium to the degenerating pelvis in *Lialis* and *Ophiodes*. The adaptive radiation and morphological separation of this group indicates antiquity. The anguroids include the Helodermatidæ, Anguidæ, Anniellidæ, and Xenosauridæ on the basis of presence of a unique muscle in the throat. *Heloderma* is related to the Anguidæ through the Eocene and Oligocene family Glyptosauridæ.

The Anniellidæ are close to *Gerrhonotus* in structure of throat musculature and hemipenes. *Ophiodes* resembles *Celestus* in the former respect. *Gerrhonotus* and *Ophisaurus* are not as closely related as the latter is to *Anguis*.

*Xenosaurus* is specialized in throat musculature and loss of the third branchial arch, and is neither intermediate between the Anguidæ and Iguanidæ, nor related to the Gekkonidæ. It is related to and probably derived from the anguids.

The Zonuridæ are not related to the Iguanidæ except as they retain the tongue and, partially, the hemipenial structure of the Ascalabota. They have the key characters of the Autarchoglossa and are included in the Anguimorpha on account of their simple clavicles and the structure of their osteoderms.

The Serpentes are believed to have arisen from anguimorphid lizards. *Paliguana* Broom of the Triassic is regarded as a lizard.

*Ardeosaurus* von Meyer of the Jurassic constitutes the type of a new family related to the geckos.

*Chamops* Marsh of the Cretaceous is believed to be related to the Iguanidæ and Agamidæ and to be intermediate between them in tooth emplacement.

The Tertiary Glyptosauridæ should be retained as a distinct family including *Placosaurus* of the Eocene of France.



The Eocene genera *Thinosaurus* Marsh and *Saniwa* Leidy are varanids as far as the shape of their vertebræ and teeth will permit us to judge.<sup>1</sup>

#### SUMMARY OF MORPHOLOGICAL POINTS

Complete branchial arches and attachments of the first arch (hyoid) to the paroccipital process are regarded as primitive characters in lizards. The Amphisbænidæ are not primitive in this respect. The extra-columella in the Amphisbænidæ is functionally enlarged probably for subterranean audition and does not represent a detached portion of the epihyoid.

The rib processes in the Amphisbænidæ, *Ophisaurus*, and *Lialis* are secondary muscle attachments and do not represent the primitive tuberculum.

Amphicœlous vertebræ, separate intercentra and the presence of sub-central arterial foramina are primitive characters. Zygosphenal articulations are secondary and do not of themselves show relationships between groups higher than the family. The form of the centra and the articular condyles has a systematic value.

The two dorsal temporal elements of the primitive lizard skull are regarded as the tabulare (inner) and squamosal (outer). Relationships with thalattosaurs and ichthyosaurs are closer in this respect than with *Sphenodon*. The single element present in geckos and other lizards in which the supratemporal arch is absent is considered the tabulare.

Remains of the shoulder-girdle are present in the Anniellidæ and Dibamidæ. The degenerating girdle in scincomorphs tends to first lose the clavicle and interclavicle. In anguimorphs, the scapulo-coracoids and interclavicles are the first to disappear. Many stages of extreme degeneration in scincomorphs correspond to early stages in the ontogeny of the pectoral girdle and sternum.

Paired skull elements are the primitive condition. After fusion all traces of separation are soon lost in the embryo (cf. Siebenrock, 1892) so that it seems unlikely that reversion can occur.

The prevomers of *Chamæleon* are often fused and sometimes paired.

Retention of ribs on the anterior cervical vertebræ is regarded as primitive. Articular facets on the cervical diapophyses are not a safe indication of the presence of corresponding ribs.

The postfrontal tends to be reduced in the Ascalabota, the post-orbital in the Autarchoglossa. There are exceptions. In the Scincimorpha the postfrontal sometimes enlarges to secondarily close the supratemporal fenestra. This does not occur in the Anguimorpha.

<sup>1</sup>Gilmore (1922, Proc. U. S. Nat. Mus.) has recently described the skull and skeleton of *Saniwa* and finds it to be remarkably similar to *Varanus*.



Thecodont dentition is considered ancestral to the present day, highly developed pleurodont and acrodon types.

Palatal teeth are best developed in the anguroids and are not known to be secondarily produced, though they are frequently increased in number and extent of area.

The interclavicle and clavicle undergo progressive reduction in various descent lines.

The throat musculature is regarded as an important index to the degree of specialization and the relationships of certain families one to another.

The glands on the surface of the papillate tongues of the Ascalabota and Anguimorpha are less specialized than those of the scaly-tongued Scincomorpha. This leads us to regard the former condition as primitive.

The elements of the lower jaw undergo fusion and reduction in specialized groups.

The caudal chevrons tend to migrate forward to the centra in the Anguimorpha, having done so in the Platynota, the Glyptosauridæ, the Anniellidæ, and in *Ophisaurus*, but retaining the primitive intercentral position in the Helodermatidæ, Pygopodidæ, Zonuridæ, Xenosauridæ, and in *Gerrhonotus*.

The presence of a separate os intermedium is regarded as primitive. Its absence or fusion is of little significance.

The superficial layer of the rectus is regarded as a primitive crawling muscle. Its presence in certain primitive agamids tends to show this and its absence in all other Ascalabota is considered secondary and possibly concerned with the arboreal tendencies of the group.

The body musculature as a whole is most highly modified in burrowing, worm-like forms and least developed in permanent arboreals, especially in *Uroplatus* and *Chamaeleon*.

The sternum is homologous in salamanders and lizards, and is formed of the anterior portions of the parasternal bars. The xiphisternum has a similar origin. Neither are they products of the ribs or the coracoids.

The parasternum is homologous in lizards, *Sphenodon*, and reptiles and amphibians. In lizards it attains a closer correspondence with the body segmentation than in early reptiles and *Sphenodon*.

Closure of the palate is secondary in lizards and is not related to the mammalian condition.

There is some anatomical evidence to show that the pineal eye may still be functional in the Scincoidea and some Anguioidea. It is certainly



non-functional as a visual organ in most other lizards. Size of the foramen is not always a safe index to the size and functional ability of the eye.

Diffuse and compound osteoderms are regarded as primitive, solid and simple osteoderms covered by a single horny scale as specialized.

Granular lepidosis and non-correspondence between ventral scale-rows and internal metamerism is considered more primitive than exact correspondence between external and internal segmentation.

The femoral organs are pseudo-glands proliferating modified epidermal cells. The secretion may serve the male to hold more firmly during copulation. Secondary development seems to occur in the Agamidæ.



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Figs. 1-7. VERTEBRÆ OF ASCALABOTA; ventral view of mid-dorsal vertebræ, the eighth forward from the sacrum.

Figs. 1-4. Gekkonidæ. The centra are squarish in ventral view and retain intercentra, ITC, and subcentral foramina. The condylar ball in the procœlous forms is small.

Figs. 5-6. Iguania. The centra taper, the intercentra and subcentral foramina are lost and the condylar ball is enlarged.

Fig. 7. Rhiptoglossa. The elongation of the cylindrical centra has proceeded beyond the point reached in the Agamidæ, Fig. 5.

Fig. 1. *Thecadactylus rapicauda*, A. M. N. H. No. 6474. The intercentrum, ITC, is partly fused with the posterior end of the amphiœlous centrum.

Fig. 1a. End view of the half-ring-shaped intercentrum.

Fig. 2. *Tarentola cubana*, A. M. N. H. No. 22727. The intercentrum, ITC, is loosely joined to the amphiœlous centrum.

Fig. 3. *Sphærodactylus macrolepis*, A. M. N. H. No. 22729.

Fig. 4. *Coleonyx variegatus*, A. M. N. H. No. 2541.

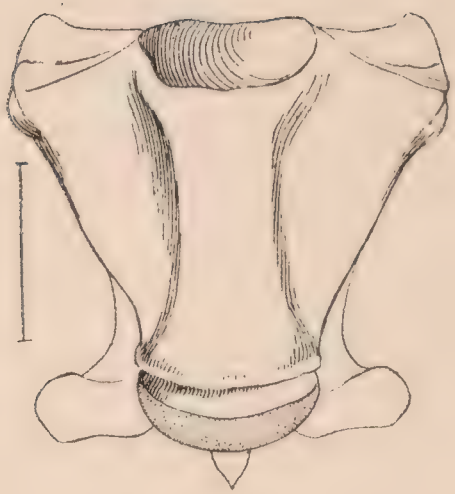
Figs. 3 and 4. Procœlous geckos in which the scale-like intercentrum remains fused to the small condyle.

Fig. 5. *Calotes versicolor*, Skel. in Dept. Herpetol., A. M. N. H.

Fig. 6. *Sauromalus hispidus*, A. M. N. H. No. 5675.

Fig. 7. *Chamæleon gracilis*, A. M. N. H. No. 11608.

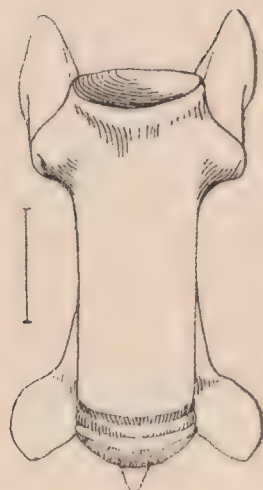




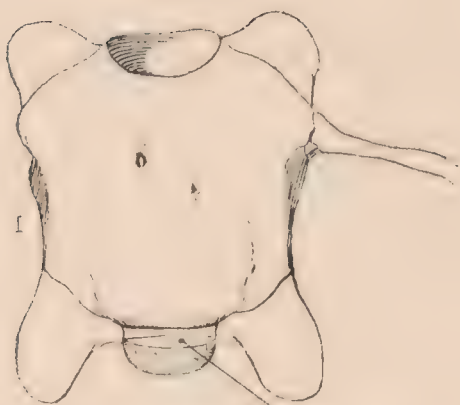
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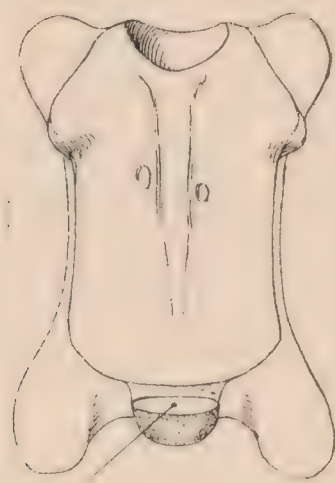
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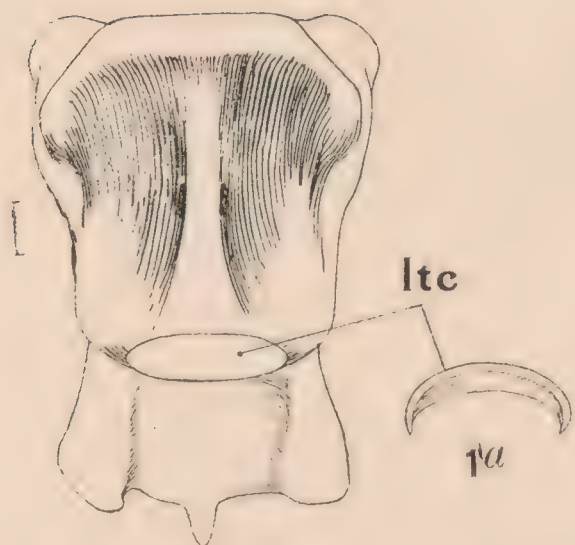
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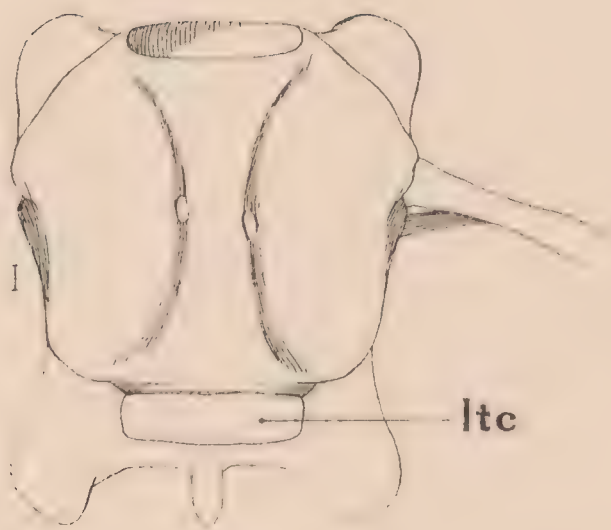
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Figs. 8-12. VERTEBRÆ OF SCINCOMORPHA; ventral view of mid-dorsal vertebræ, the eighth forward from the sacrum.

Fig. 8. *Xantusia vigilis*, A. M. N. H. No. 9204. (Cf. Fig. 4, *Coleonyx*.)

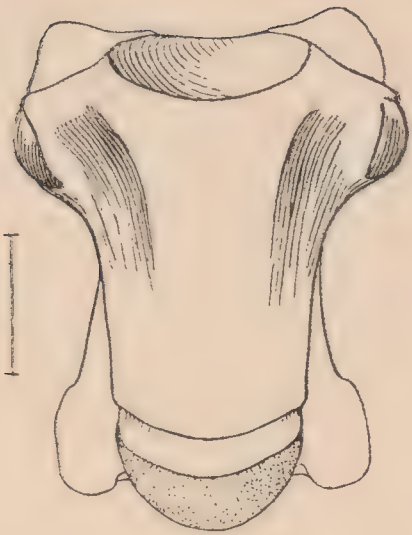
Fig. 9. *Amphisbæna alba*, A. M. N. H. No. 8747.

Fig. 10. *Tupinambis nigropunctatus*, A. M. N. H. No. 2246.

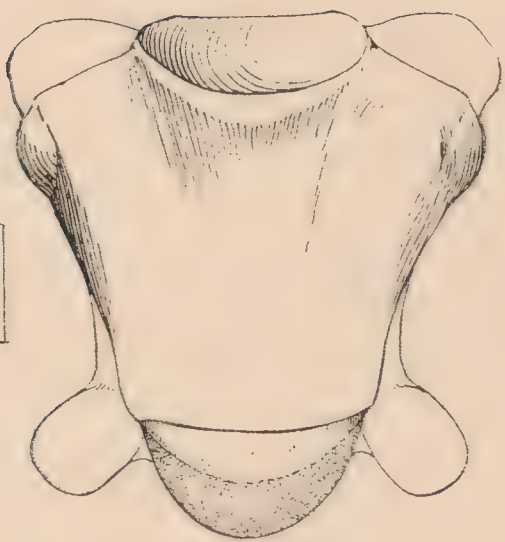
Fig. 11. *Trachysaurus rugosus*, Skel. in Dept. Herpetol., A. M. N. H.

Figs. 2-4 and 8 drawn from specimens prepared by Dr. G. K. Noble.

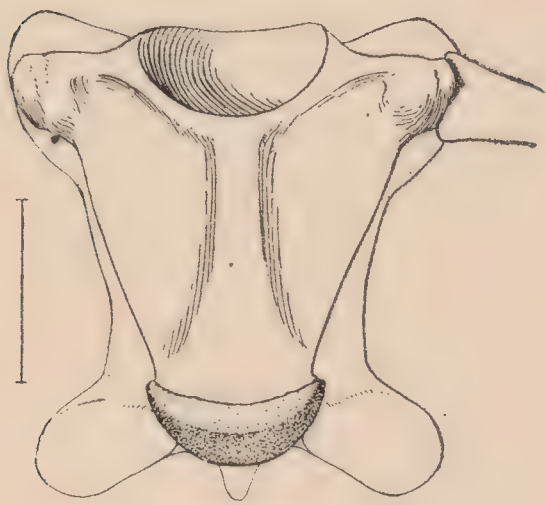




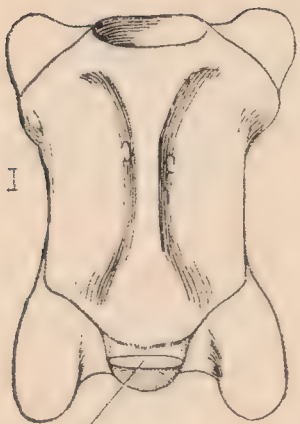
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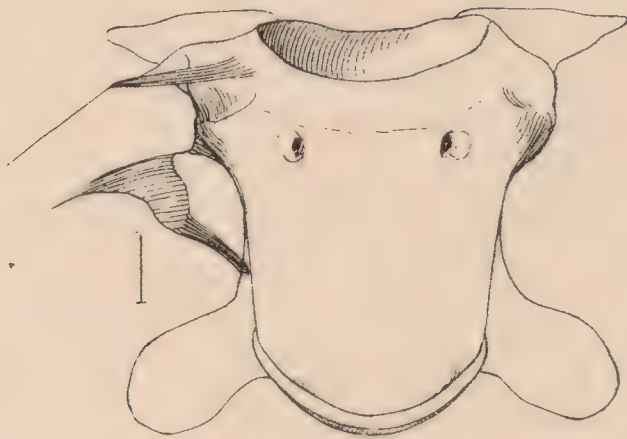


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Figs. 13-21. VERTEBRÆ AND RIBS OF ANGUIMORPHA, ventral view. Mid-dorsal vertebræ, the eighth forward from the sacrum.

Fig. 13. *Lialis burtonii*, A. M. N. H. No. 30.

Fig. 14. *Ophisaurus* sp.?, Skel. in Dept. Comp. Anat., A. M. N. H.

Fig. 15. *Gerrhonotus scincicauda scincicauda*, A. M. N. H. No. 595.

Fig. 16. Left rib of *Gerrhonotus*, dorsal view, showing ligaments of attachment and lack of muscular processes.

Fig. 17. Right rib of *Lialis*, dorsal view, showing ventral process of attachment of subvertebral muscles.

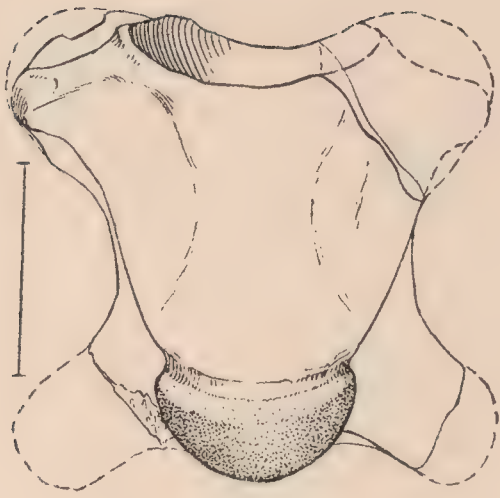
Fig. 18. Right rib of *Amphisbæna* showing posterior process for attachment of dorsal muscles (cf. Fig. 9).

Fig. 19. Right rib of *Ophisaurus* showing posterior process for attachment of dorsal muscles (cf. Fig. 14).

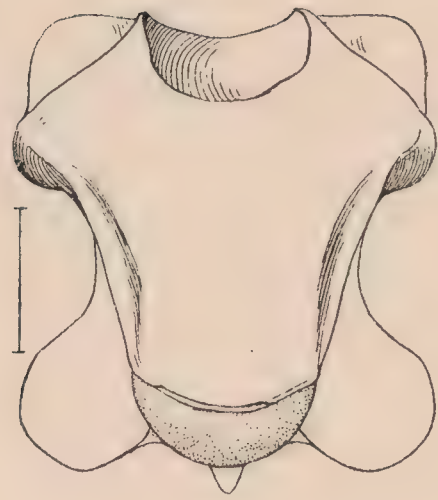
Fig. 20. Mid-dorsal vertebra of a glyptosaurid, Dept. Vert. Pal., A. M. N. H. No. 5109, Wind River, Lower Eocene.

Fig. 21. *Heloderma* sp.?, Skel. in Dept. Comp. Anat., A. M. N. H.





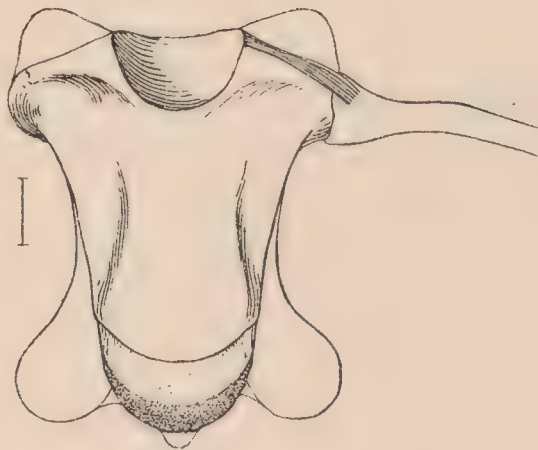
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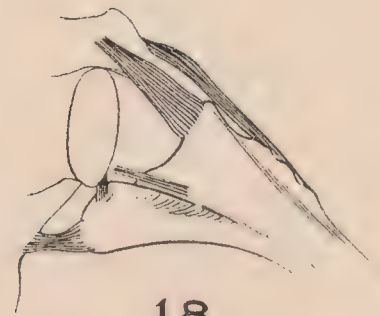
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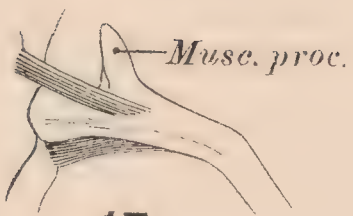
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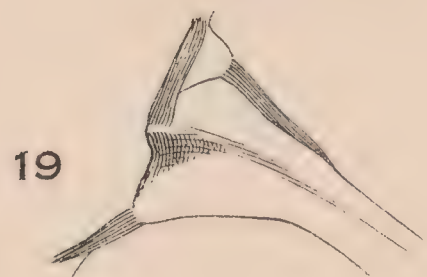
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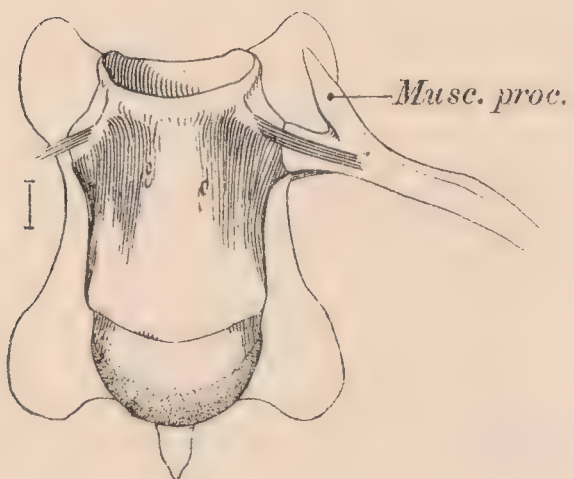
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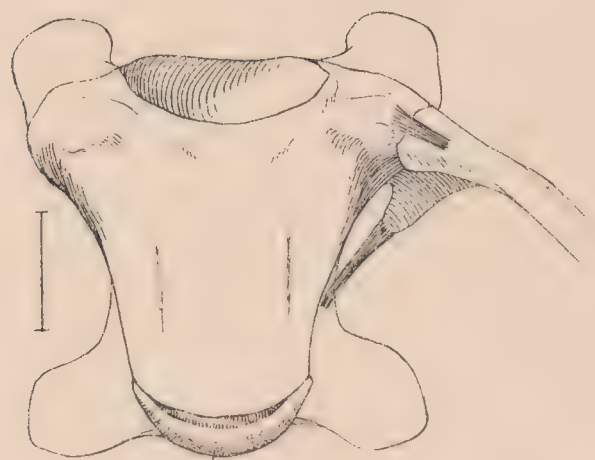
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Figs. 22-26. MID-DORSAL VERTEBRÆ OF PLATYNOTA.

Fig. 22. *Clidastes westii*,  $\times \frac{1}{2}$ , after Williston (1898, Pl. LIII, fig. 2).

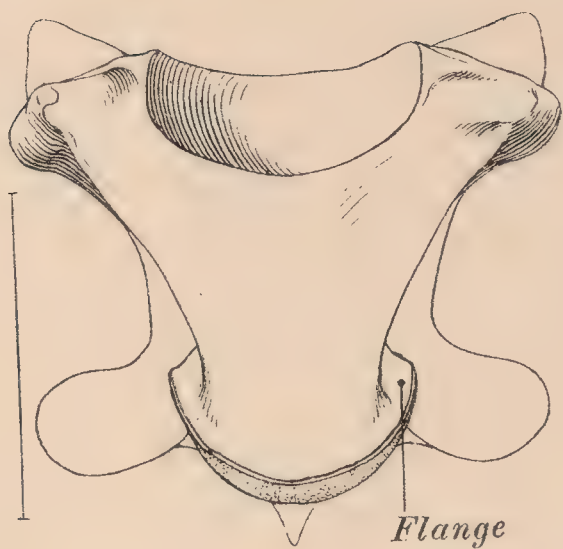
Fig. 23. *Thinosaurus* sp.? Dept. Vert. Pal., A. M. N. H. No. 6057.

Fig. 24. *Saniwa* sp.?, Dept. Vert. Pal., A. M. N. H. No. 6056.

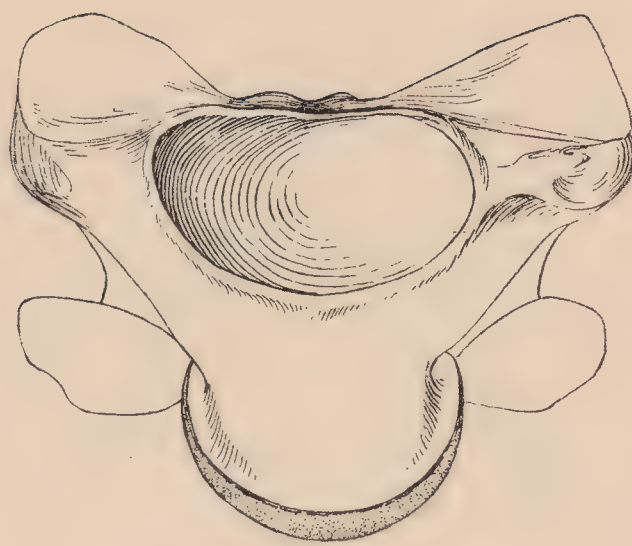
Fig. 25. *Varanus niloticus*, Skel. in Dept. Herpetol., A. M. N. H.

Fig. 26. *Megalanina prisca*,  $\times \frac{1}{6}$ , after Fejérváry (1918, Fig. 34d, p. 458, from an original figure by R. Owen).

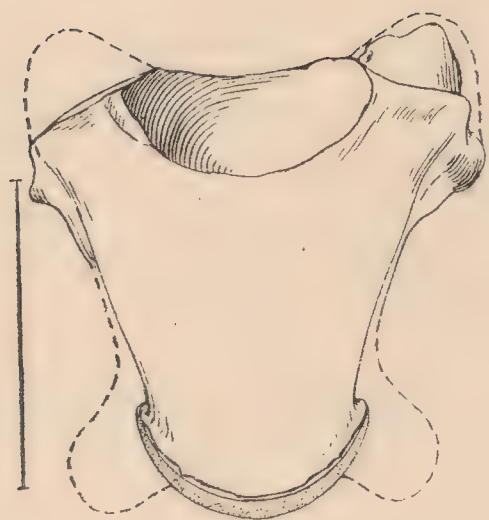




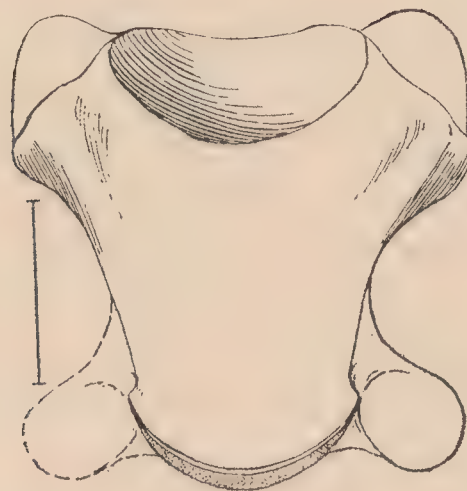
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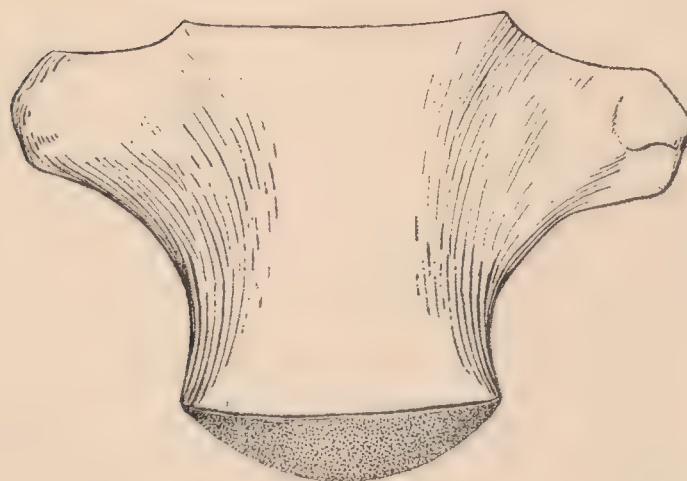
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Figs. 27-31. HYOID APPARATUS OF ASCALABOTA.

Fig. 27. *Coleonyx variegatus*,  $\times 4\frac{1}{2}$ , A. M. N. H. No. 2538. The three arches are complete, the first and third being connected with the paroccipital process. All parts are cartilaginous with exception of the second arch.

Fig. 28. *Uroplates fimbriatus*,  $\times 1\frac{3}{4}$ , A. M. N. H. No. 2235. The second epibranchial remains as a short cartilage connected with a posterior slip of the Hyoglossus muscle. The epihyal is joined to the paroccipital process.

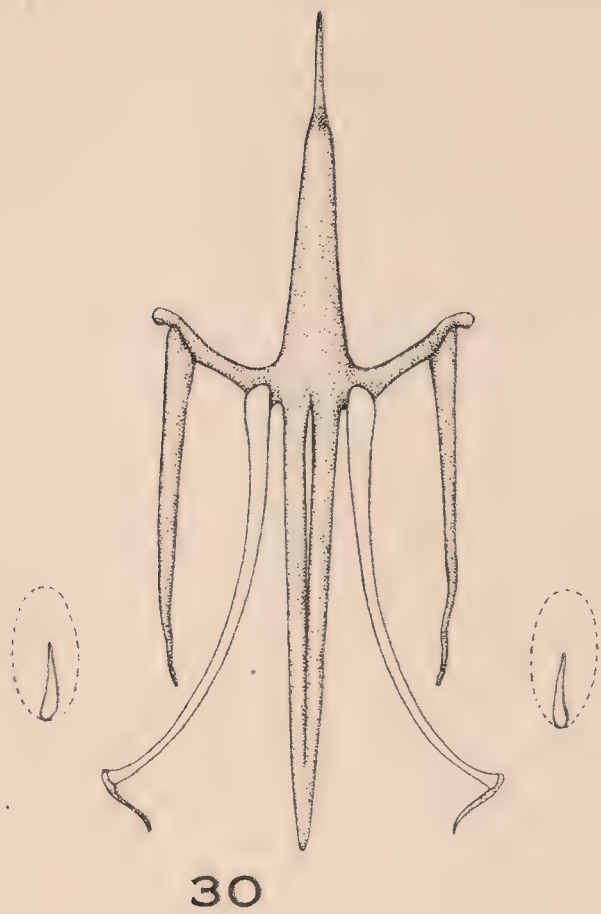
Fig. 29. *Brachylophus fasciatus*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 17701. The second ceratobranchial is enlarged, as in many Iguania, for support of the throat fan. The second epibranchial is absent.

Fig. 30. *Calotes versicolor*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 2147. This agamid is similar to the arboreal iguanids in form of the hyoid but the ceratohyal is relatively more reduced.

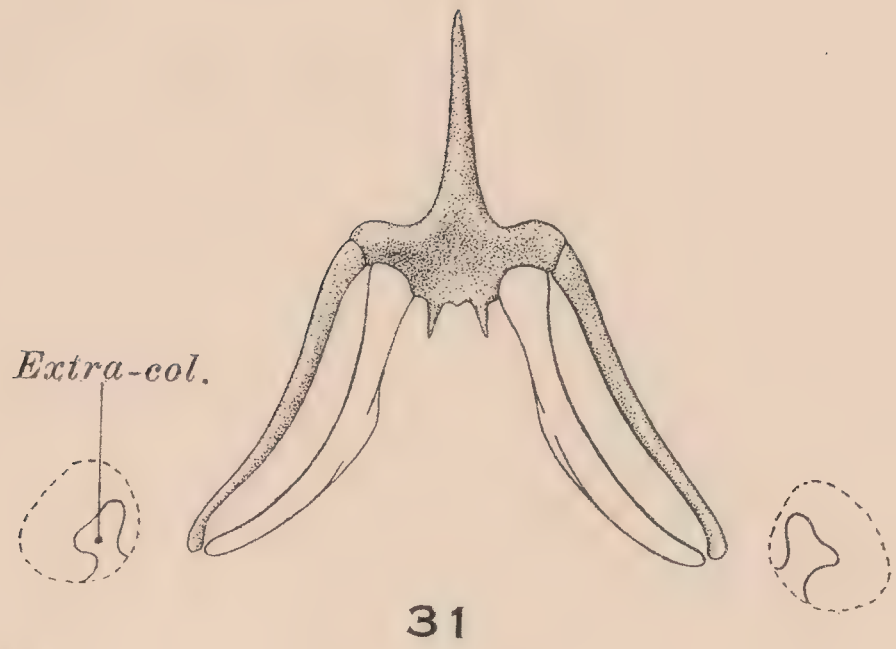
Fig. 31. *Phrynosoma hernandesi*,  $\times 2\frac{1}{4}$ , A. M. N. H. No. 583. Shows extreme reduction for an iguanian.

*Ceratobr.* = Ceratobranchial  
*Ceratohy.* = Ceratohyal  
*Extra-col.* = Extra-columella

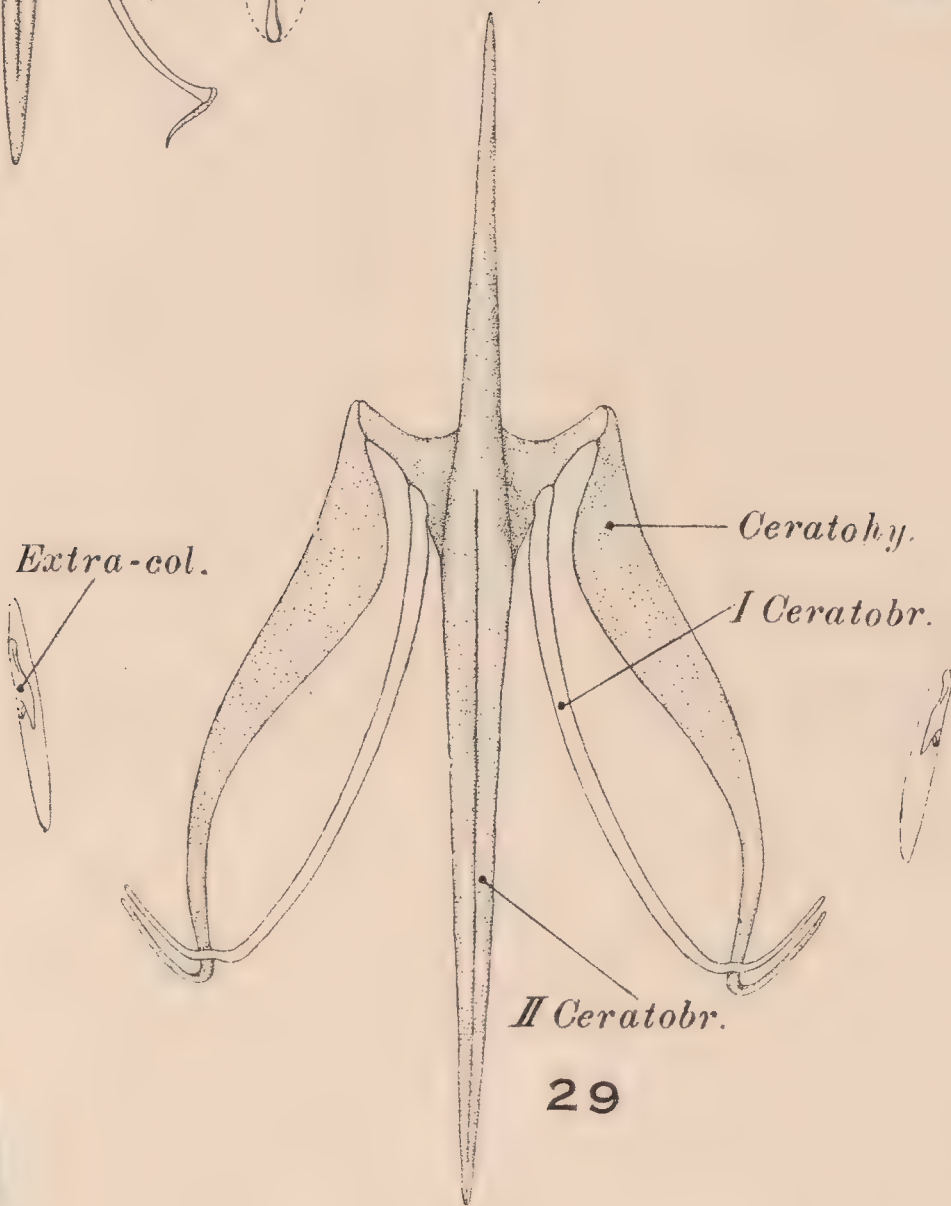




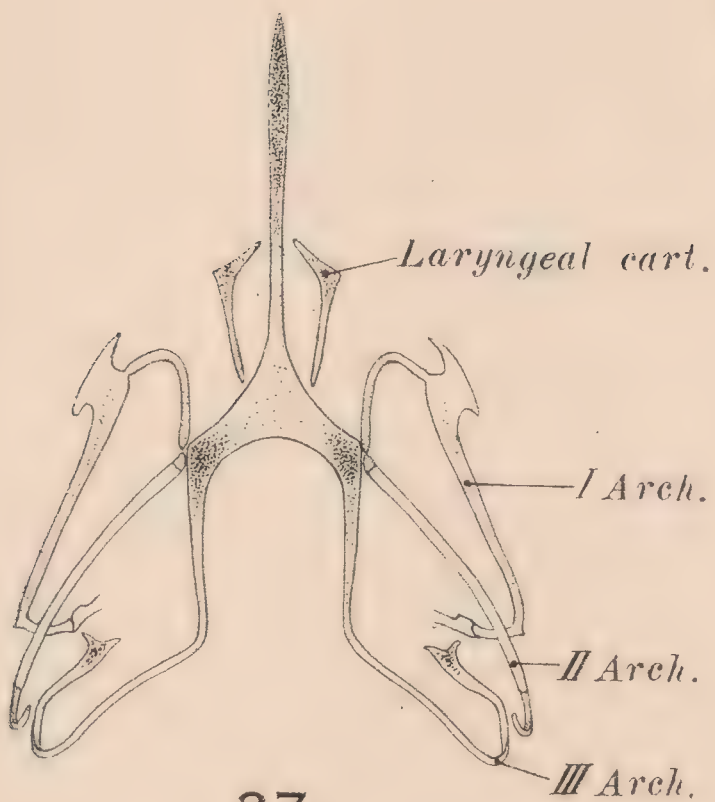
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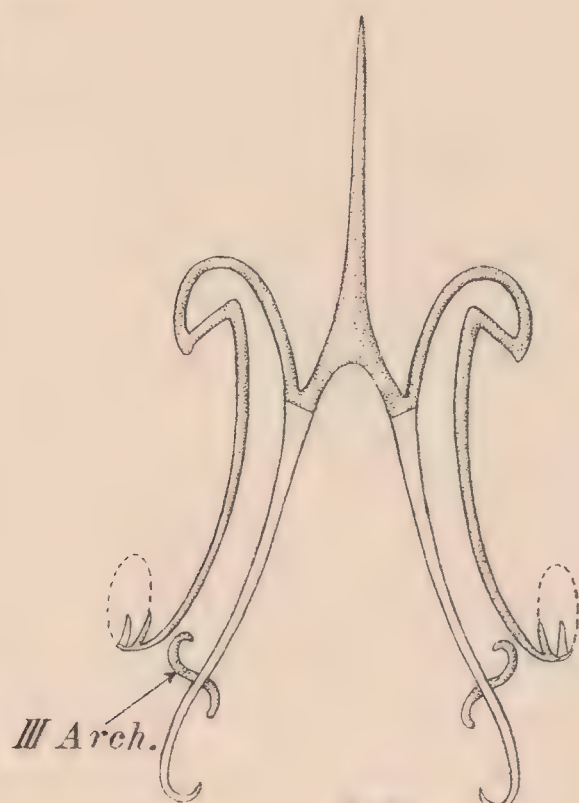
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Figs. 32-37. HYOID APPARATUS OF AUTARCHOGLOSSA.

Fig. 32. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 10721. Hyoid and first branchial arches attached to the paroccipital. Second epibranchial attached to the exoccipital.

Fig. 33. *Gerrhonotus scincicauda webbiai*,  $\times 2$ , A. M. N. H. No. 9159. Hyoid and second branchial arches loosely attached to the paroccipital process.

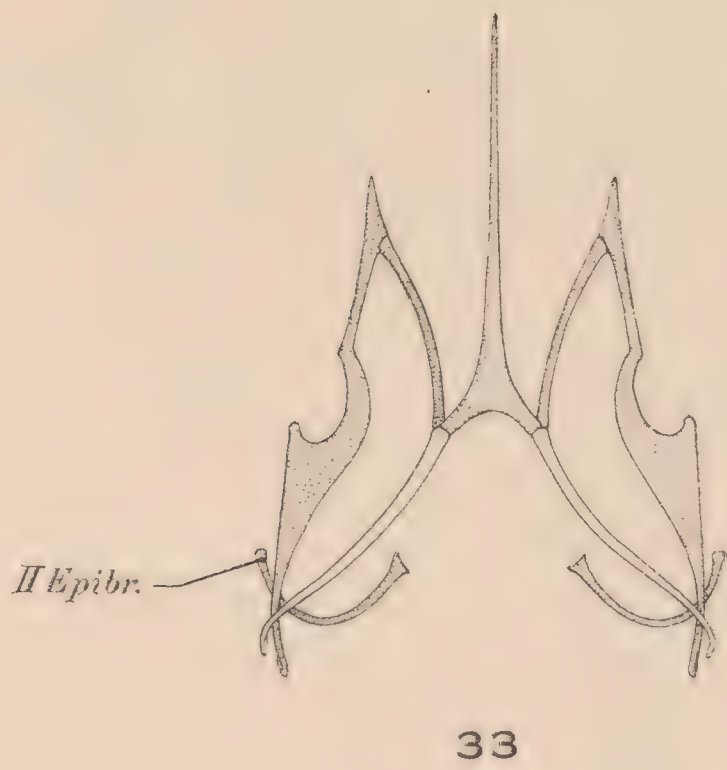
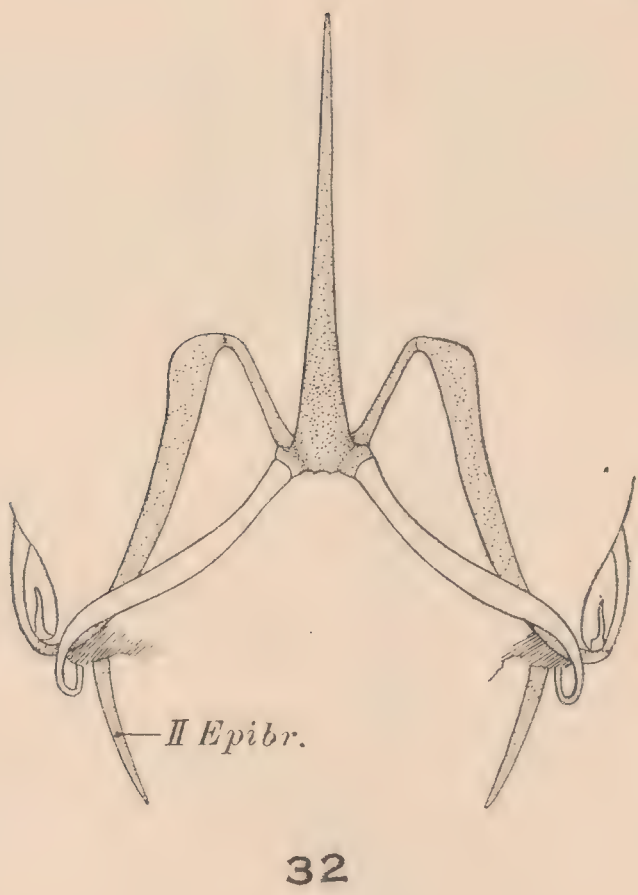
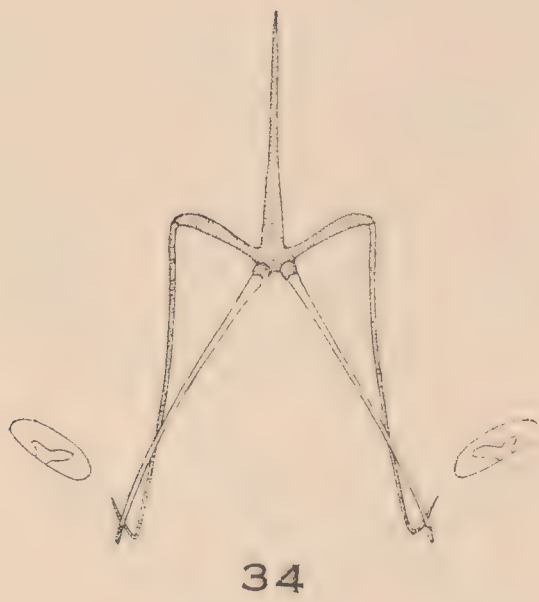
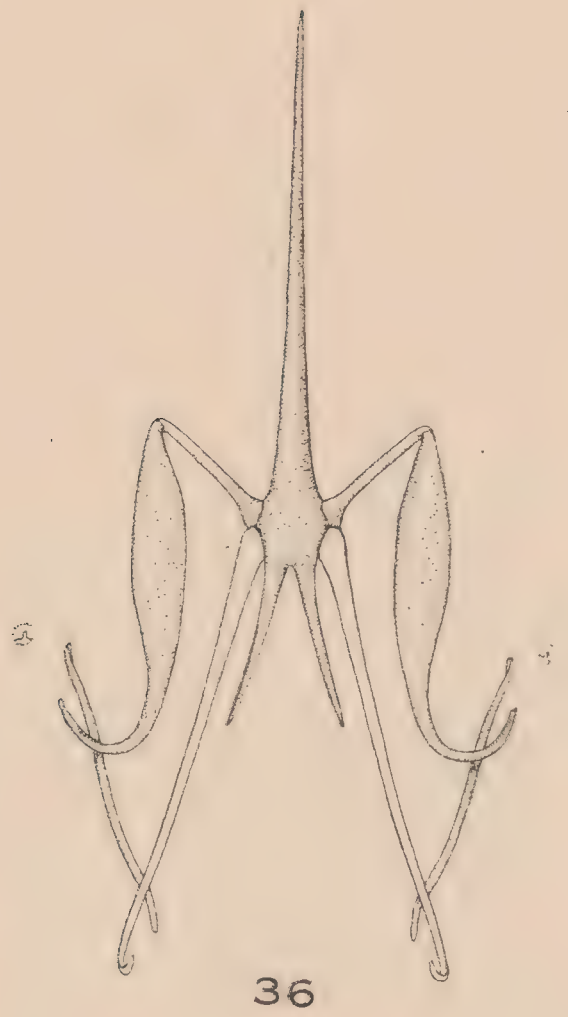
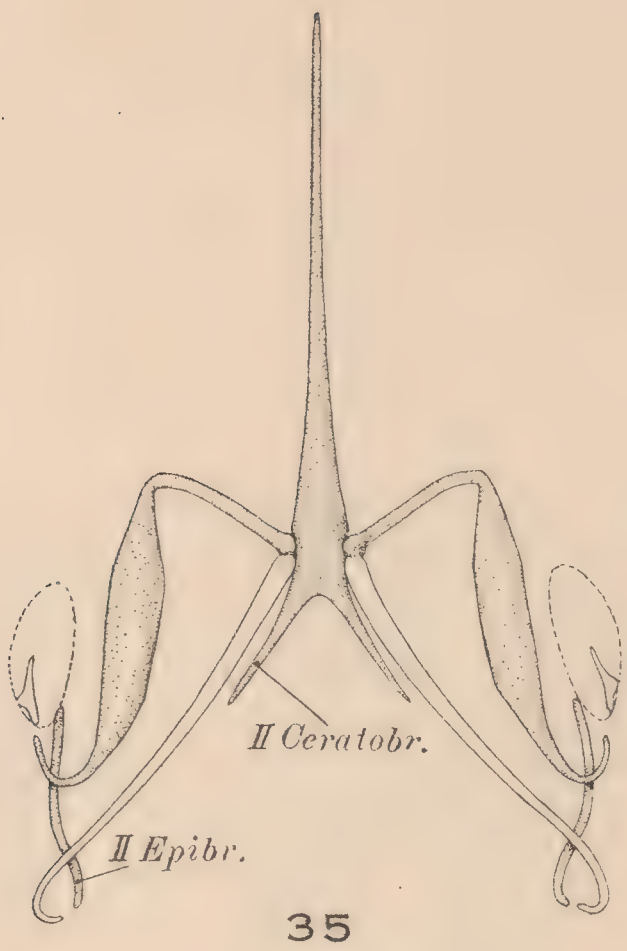
Fig. 34. *Xenosaurus grandis*,  $\times 2$ , A. M. N. H. No. 19381. No elements of the third arch remain.

Fig. 35. *Zonurus giganteus*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 8736.

Fig. 36. *Chamæsauro macrolepis*,  $\times 4$ , A. M. N. H. No. 2398. Showing close resemblance to *Zonurus*.

[Fig. 37. Omitted by author.]







Figs. 38-41. THROAT MUSCLES OF REPTILIA, for comparison with those of lizards.

Fig. 38. *Sphenodon punctatus*,  $\times .85$ , after Ruge (Festschrift für Gegenbaur, III, 1897, Figs. 61, p. 324), checked with a specimen in the Dept. Invert. Zoöl., A. M. N. H. The Mylohyoideus is in a single continuous layer and entirely underlies the Geniohyoideus. There is no Cervicomandibularis.

Fig. 39. *Crocodylus americanus*,  $\times .65$ , A. M. N. H. No. 19866. The Mylohyoideus is arranged as in *Sphenodon*. There is no Cervicomandibularis.

Fig. 40. *Amphisbæna alba*,  $\times 2$ , A. M. N. H. No. 8747. This lizard, though highly specialized, shows the typically saurian interdigitation of the Geniohyoideus with the Mylohyoideus, the separation of the latter into anterior and posterior portions and the presence of a Cervicomandibularis.

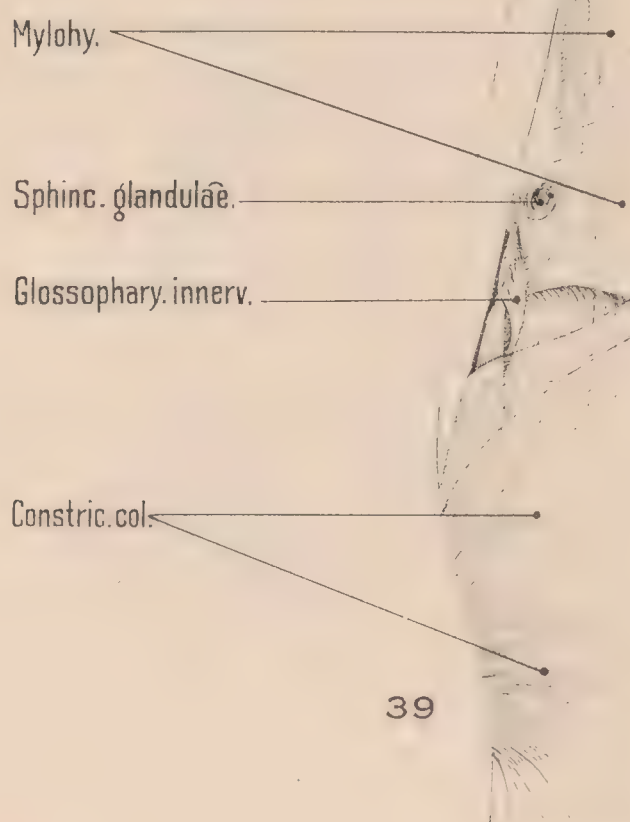
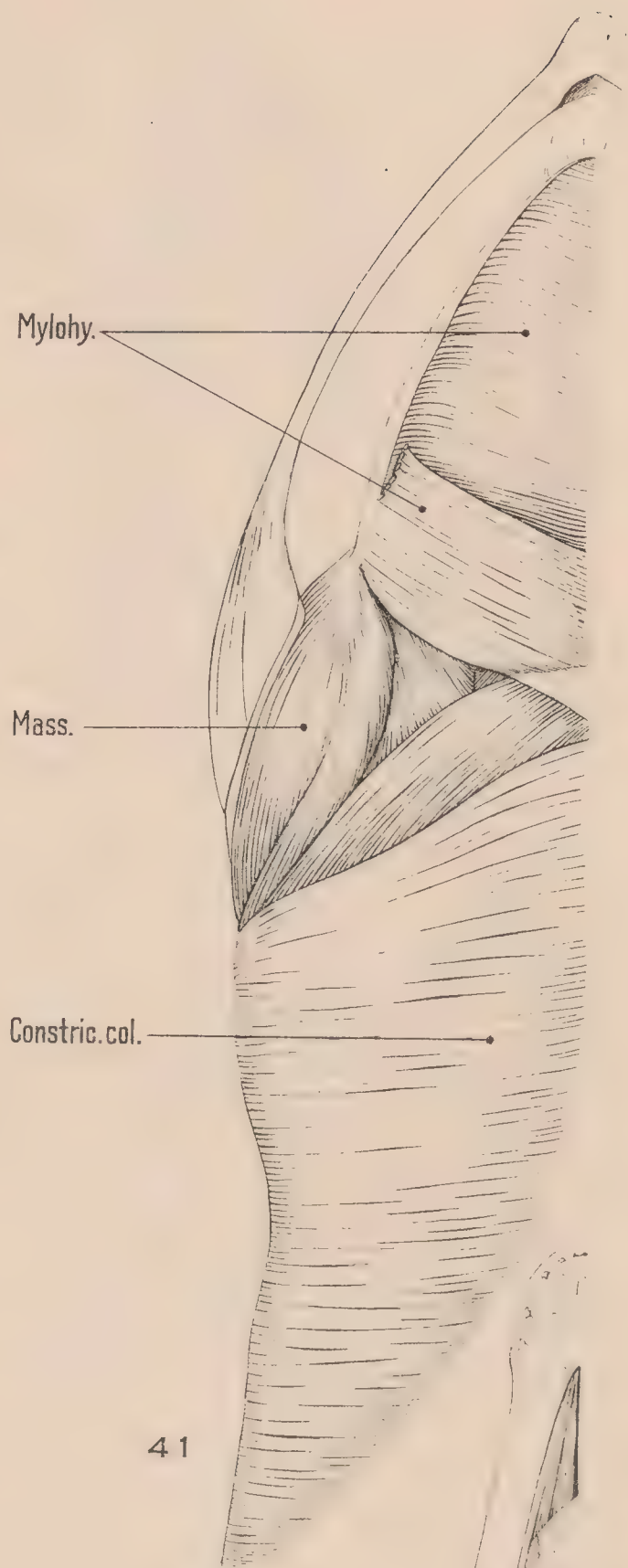
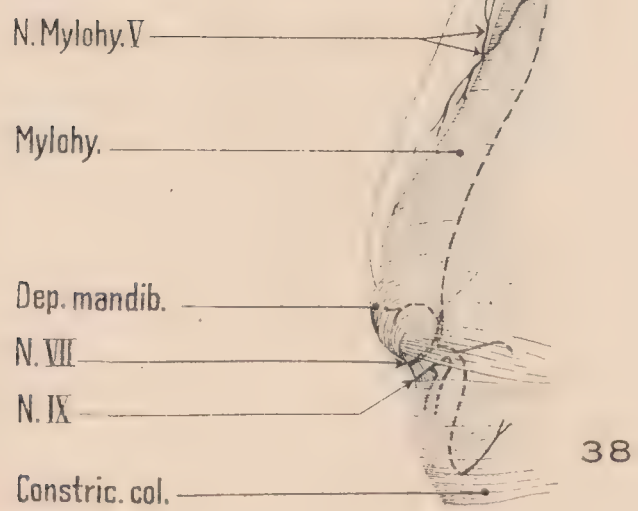
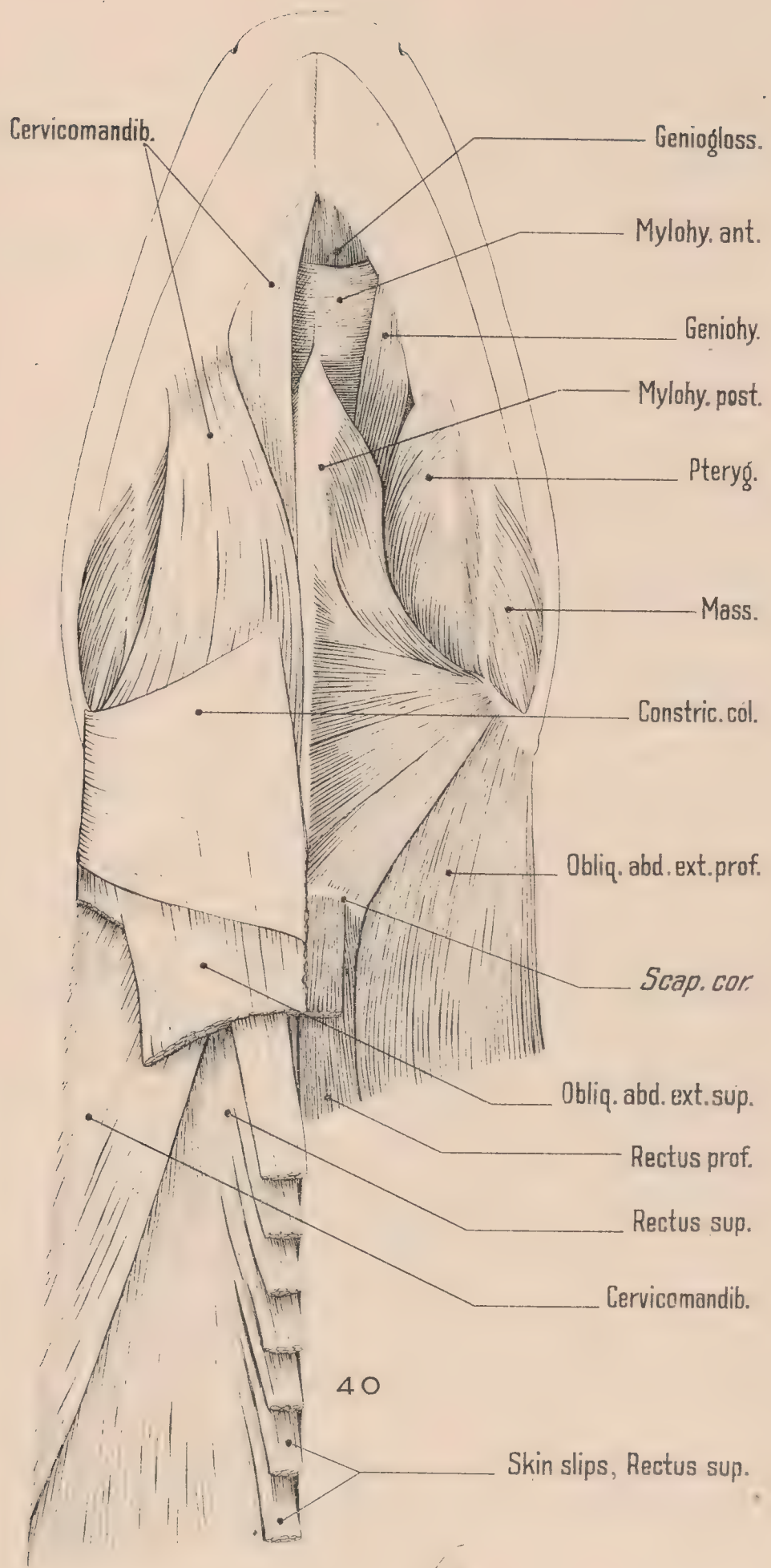
In comparison with other lizards the following points may be noted. The Cervicomandibularis is extensive. This muscle pulls the head sideways and downward as the animal forces its way through the soil. The muscle is greatly developed in all permanently subterranean lizards as are usually the body muscles shown here,—Obliquus abdominis externus superficialis which attaches closely to the skin over nearly the whole body; Obliquus externus profundus which extends forward to gain an attachment to the head; Rectus superficialis which sends slips to the skin to facilitate backward locomotion.

Fig. 41. *Chelydra serpentina*,  $\times 1$ , A. M. N. H. No. 22716. The Mylohyoideus does not interdigitate with the Geniohyoideus, and there is no Cervicomandibularis.

#### Abbreviations for Figs. 38-61

CERVICOMANDIB.=Cervicomandibularis. CONSTRIC. COL.=Constrictor colli. DEP. MANDIB.=Depressor mandibularis. EPIBR.=Epibranchial. GENIOGLOSS.=Genioglossus. GENIOMY.=Genio-myioideus. GENIOHY.=Geniohyoideus. HY.=Hyoid arch. HYOGLOSS.=Hyoglossus. INTERMAX.=Intermaxillaris. MASS.=Masseter. MYLOHY. ANT. PRINCIP.=Mylohyoideus anterior principalis. MYLOHY. ANT. PROF.=Mylohyoideus anterior profundus. MYLOHY. ANT. SUP.=Mylohyoideus anterior superficialis. MYLOHY. POST.=Mylohyoideus posterior. OBLIQ. ABD. EXT. PROF.=Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP.=Obliquus abdominis externus superficialis. OMOHY.=Omohyoideus. RECTUS PROF.=Rectus profundus. RECTUS SUP.=Rectus superficialis. SCAP. COR.=Scapulo-coracoid. SPHINC. GLANDULÆ.=Sphincter glandulæ. STERNOCLEIDOM.=Sternocleidomastoideus. STERNOHY.=Sternohyoideus. STERNOTHY.=Sternothyreioideus. STYLOHY.=Stylohyoideus (posterior part of Mylohyoideus posterior).







Figs. 42-47. THROAT MUSCLES OF ASCALABOTA.

Fig. 42. *Coleonyx variegatus*,  $\times 2\frac{3}{4}$ , A. M. N. H. No. 2538 (cf. Fig. 62). The Gekkonidæ resemble the scincomorphs in the great number of interdigitations of the Mylohyoideus anterior with the Geniohyoideus, perhaps a primitive feature.

Fig. 43. *Uroplates fimbriatus*,  $\times 1$ , A. M. N. H. No. 2235. A specialized gecko-noid (Uroplatidæ). All the muscles are excessively thin.

Fig. 44. *Brachylophus fasciatus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 17701. An iguanid, of the *Cyclura-Ctenosaura-Iguana* group, showing the well-separated, superficial bundle of the Mylohyoideus anterior characteristic of that division of the family. The Cervicomandibularis is absent in this genus.

Fig. 45. *Phrynosoma hernandesi*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 583. Shows the Mylohyoideus anterior superficialis as scarcely separable from the Mylohyoideus anterior principalis, a feature of the genera *Holbrookia*, *Callisaurus*, *Uma*, *Chalarodon*, *Crotaphytus*, and, to a lesser extent, of *Uta* and *Sceloporus*.

Fig. 46. *Calotes versicolor*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 2147 (cf. Fig. 47).

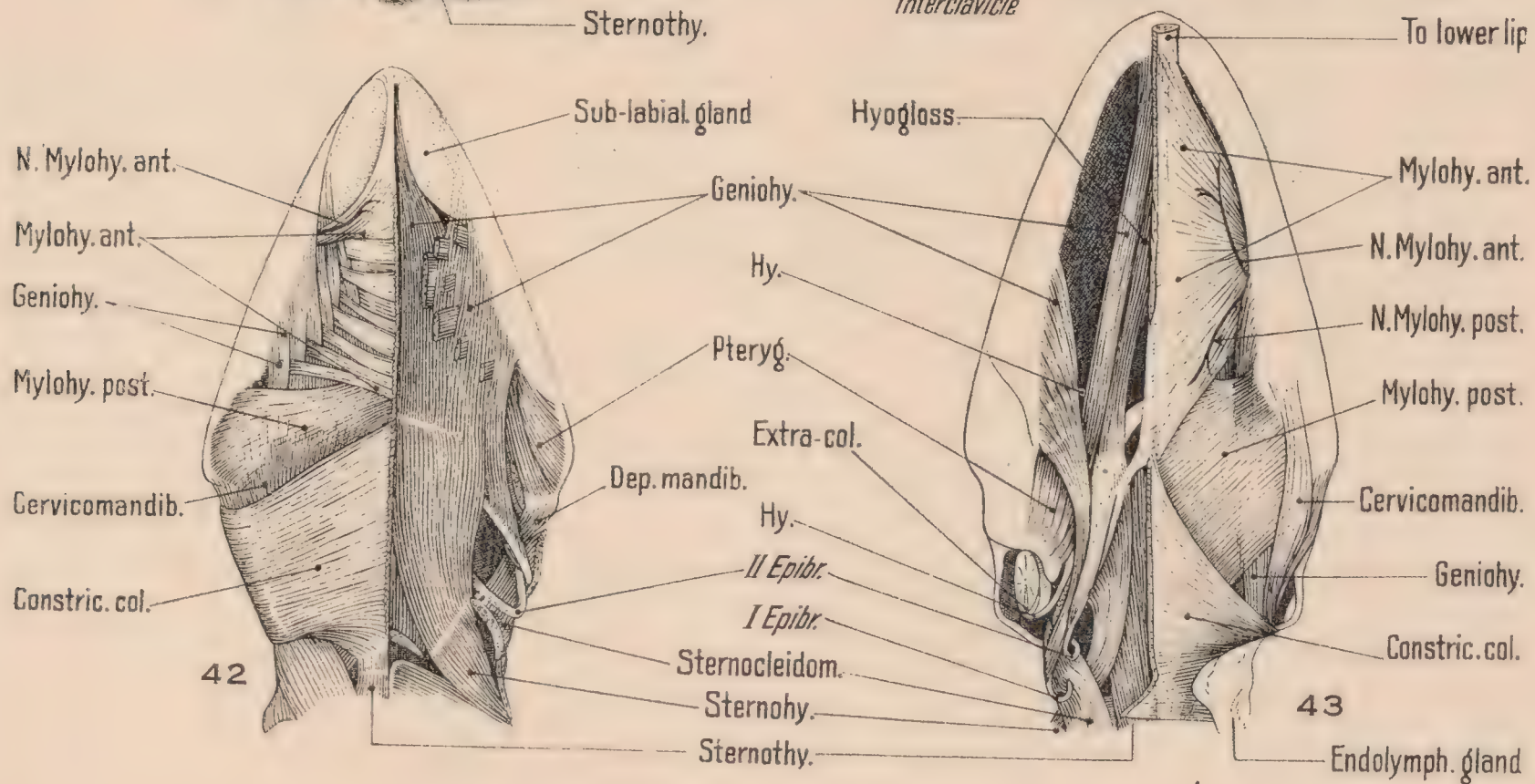
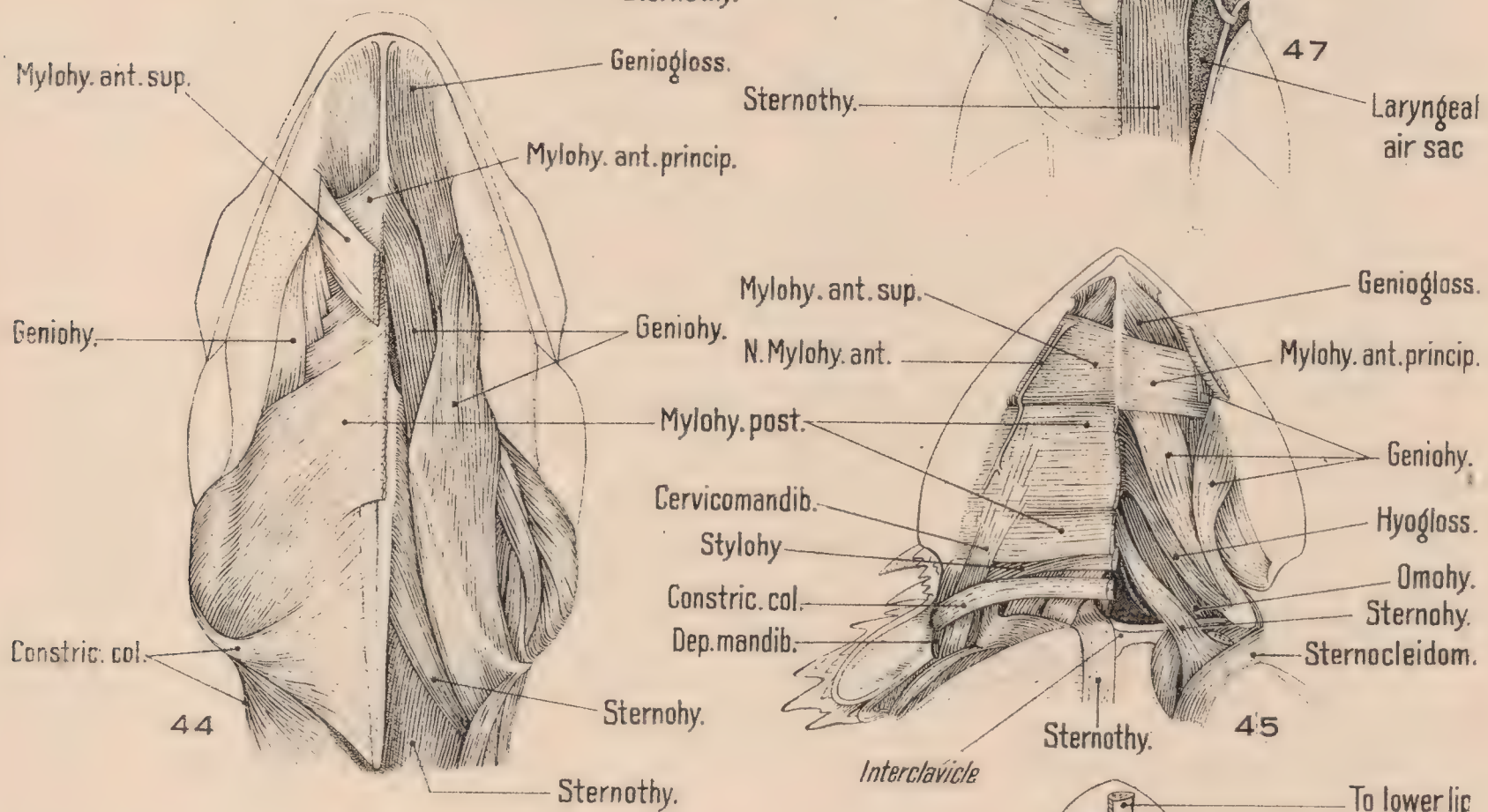
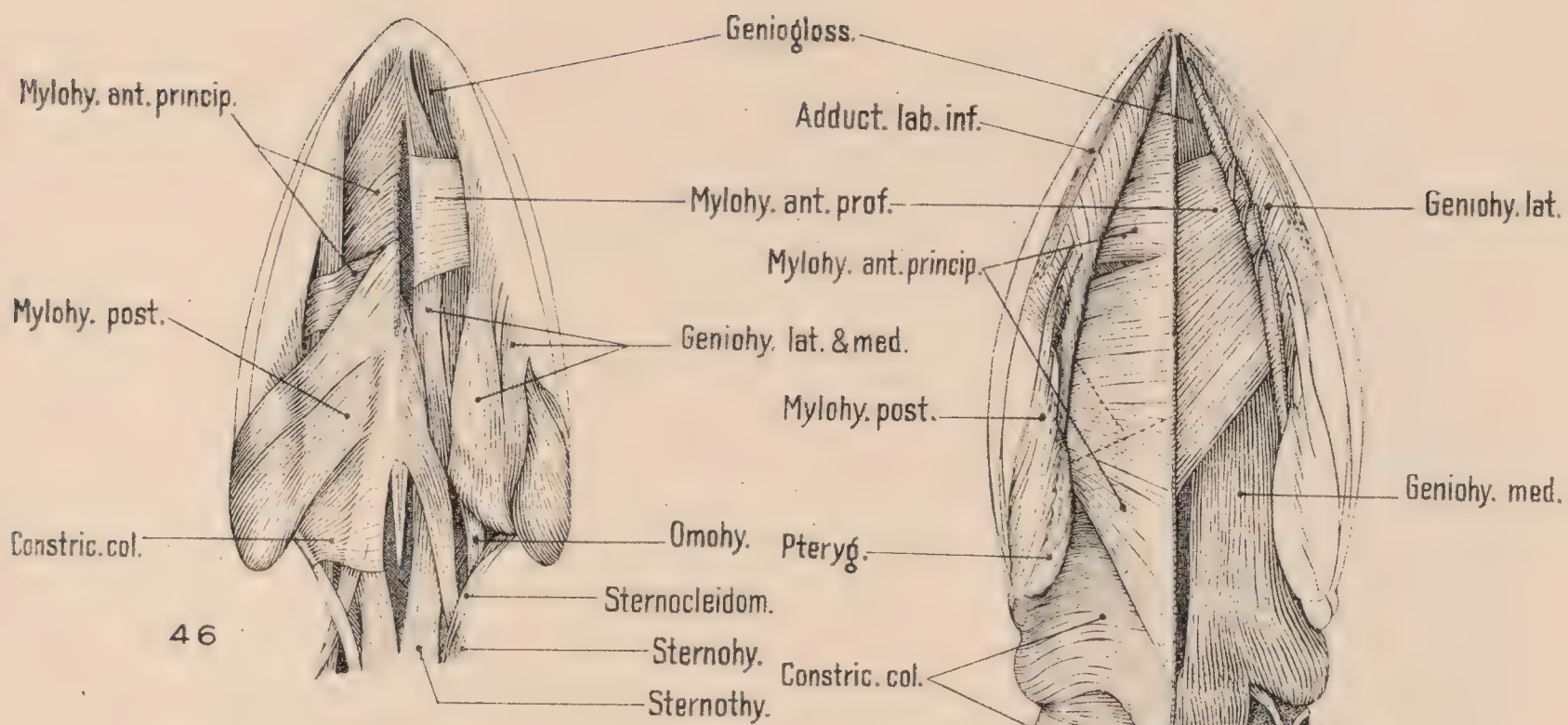
Fig. 47. *Chamæleon gracilis*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 11313.

Chameleons and agamids differ from other lizards in having an internal layer, the Mylohyoideus anterior profundus, lying dorsal to the Mylohyoideus anterior principalis. The latter always interdigitates with the Geniohyoideus lateralis. The Mylohyoideus anterior superficialis is absent in agamids and chameleons. The Cervicomandibularis is absent in the highly arboreal agamids and in the chameleons, and in both, the Mylohyoideus posterior runs obliquely forward over the Mylohyoideus anterior.

Features apparently peculiar to chameleons are the forward extension of the Constrictor colli, the great breadth of the Mylohyoideus anterior principalis, and the reduction of the Mylohyoideus posterior.

For abbreviations see p. 448.







Figs. 48-52. HYOID MUSCLES OF SCINCOMORPHA.

Fig. 48. *Xantusia riversiana*,  $\times 2$ , No. 7072, Mus. Vert. Zoöl. The Cervico-mandibularis is very broad as in *Coleonyx*; otherwise the arrangement of the muscles is not geckoidean.

Fig. 49. *Trachysaurus rugosus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 2046.

Fig. 50. *Lacerta ocellata*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 1731.

Fig. 51. *Tupinambis nigropunctatus*,  $\times .8$ , A. M. N. H. No. 1932.

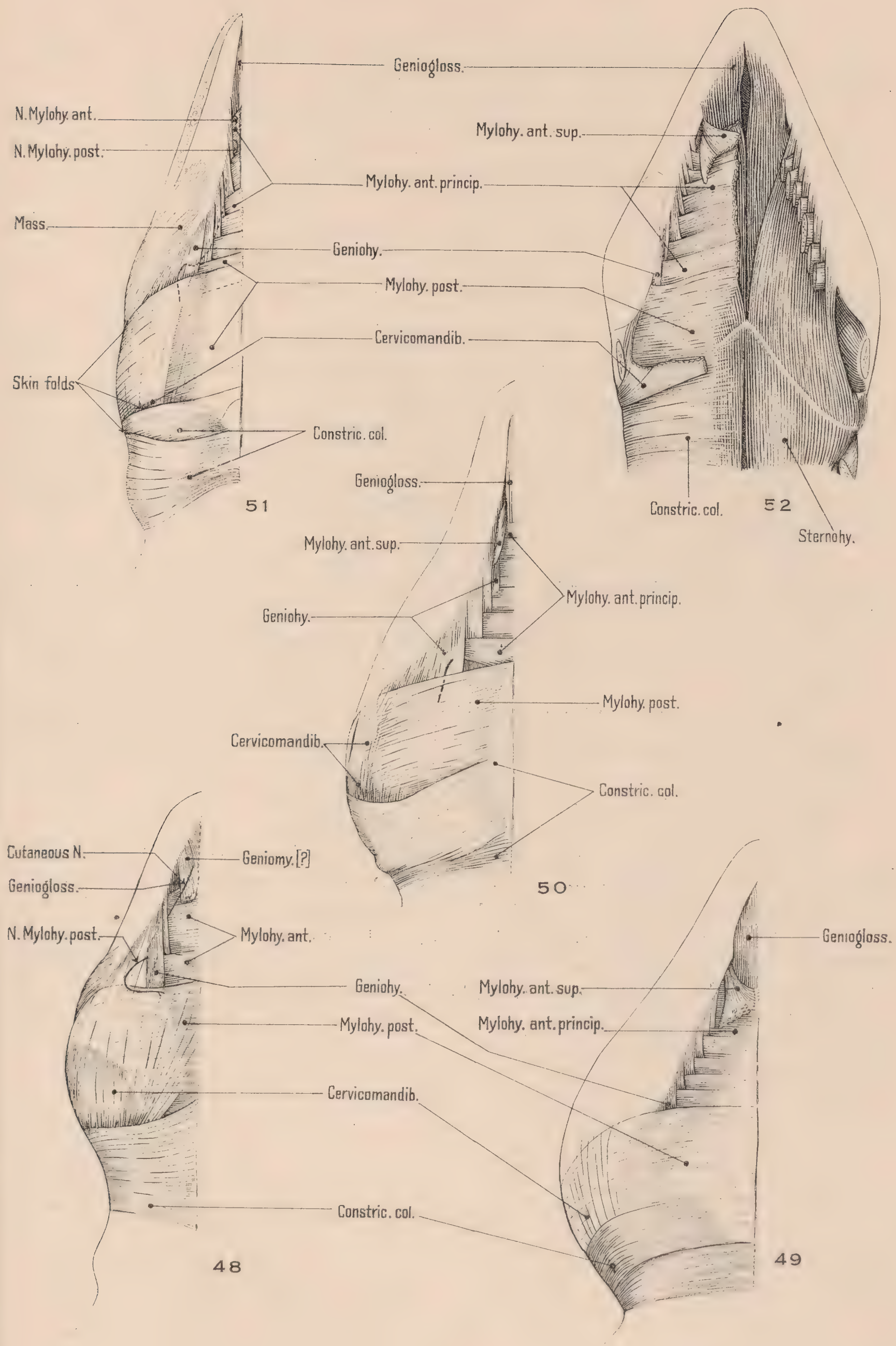
Fig. 52. *Gerrhosaurus zechi*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 10721.

Typical scincomorphid characters are the large number of regular and closely placed interdigitations of the Mylohyoideus anterior and posterior, the directly transverse fibers of these muscles, and their unbroken continuity. Resemblances are closest between the scinc, *Trachysaurus*, the lacertid, *Lacerta*, and the gerrhosaurid, *Gerrhosaurus*. Each of these has a small reflected anterior slip of the Mylohyoideus anterior.

The skin folds on the throat of *Tupinambis* join the edges of the muscles along the lines indicated.

For abbreviations see p. 448.







Figs. 53-57. THROAT MUSCLES OF ANGUIMORPHA AND SERPENTES.

Fig. 53. *Typhlops congestus*,  $\times 3$ , A. M. N. H. No. 11664. This burrowing snake has saurian resemblances in the presence of a typical Cervicomandibularis, an interdigitation of Geniohyoideus, and Mylohyoideus with consequent separation of the latter into anterior and posterior portions. In addition there is a reflected portion of Mylohyoideus anterior. The Intermaxillaris may represent the Geniomyoideus of the Anguioidea (cf. Figs. 58-61).

Fig. 54. *Varanus nuchalis*,  $\times .8$ , A. M. N. H. No. 620. The Constrictor colli is divided by a longitudinal raphe. This is known elsewhere only in *Blanus cinereus* (cf. Smalian, 1885). Other features in common with the Amphisbænidae are the forward continuation of Mylohyoideus posterior, the deeply set Mylohyoideus anterior, and the division of the anterior tendons of the Cervicomandibularis into two parts (cf. Fig. 40).

The Geniohyoideus, Mylohyoideus posterior and Cervicomandibularis are peculiarly arranged, apparently to act upon the sutural articulation across the middle of the lower jaw.

Fig. 55. *Zonurus giganteus*,  $\times 1\frac{1}{4}$ , A. M. N. H. No. 8736.

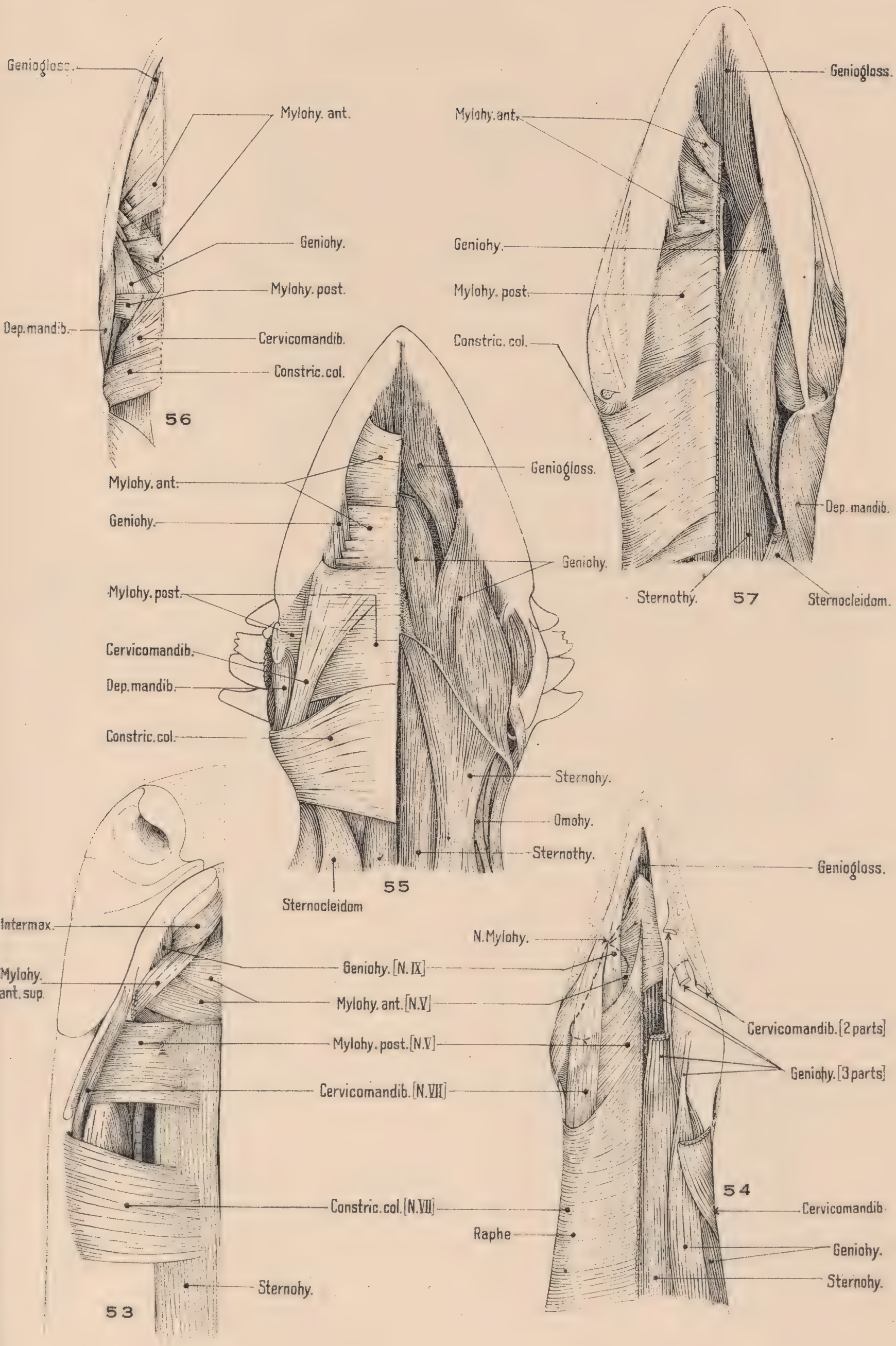
Fig. 56. *Lialis burtonii*,  $\times 2$ , A. M. N. H. No. 30.

The arrangement is peculiar and suggests that seen in *Uroplatus*. Differences between *Lialis* and *Chamæsauro* are not great enough to prohibit relationship with the Diploglossa which other points in the structure suggest.

Fig. 57. *Chamæsauro macrolepis*,  $\times 3$ , A. M. N. H. No. 2398. Similarities between these two genera include restriction of the interdigitating portion of the Geniohyoideus, lack of separation of parts of the Mylohyoideus.

For abbreviations see p. 448.







Figs. 58-61. THROAT MUSCLES OF THE ANGUIOIDEA, a well-united group on the basis of the throat musculature. A peculiar feature is the presence of the Genio-myoideus, a superficial derivative of the Genioglossus. A character uniting *Gerrhonotus*, *Anniella*, and *Xenosaurus* is the division of the Mylohyoideus into four distinct parts.

Fig. 58. *Heloderma suspectum*,  $\times .8$ , A. M. N. H. No. 804.

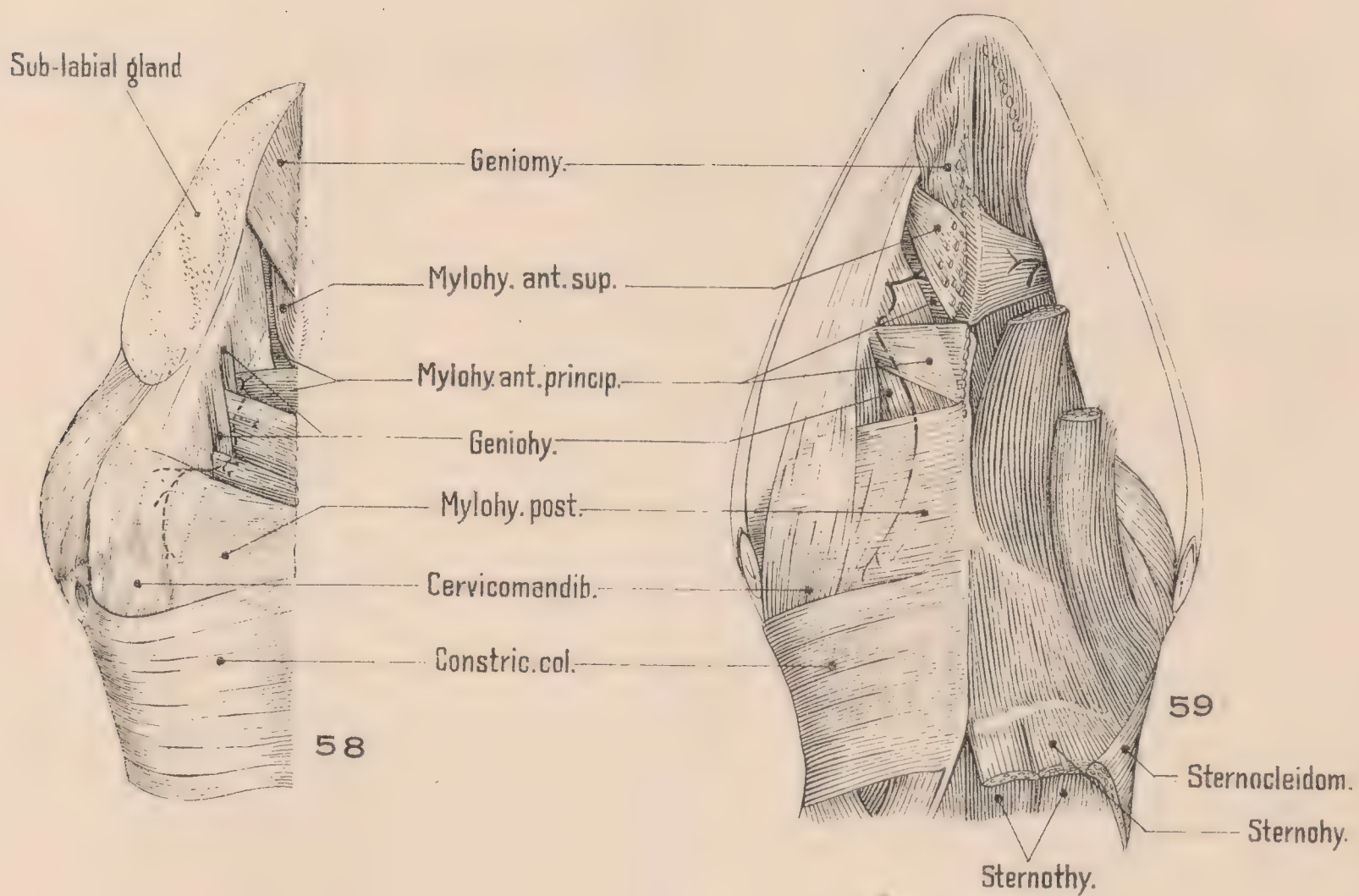
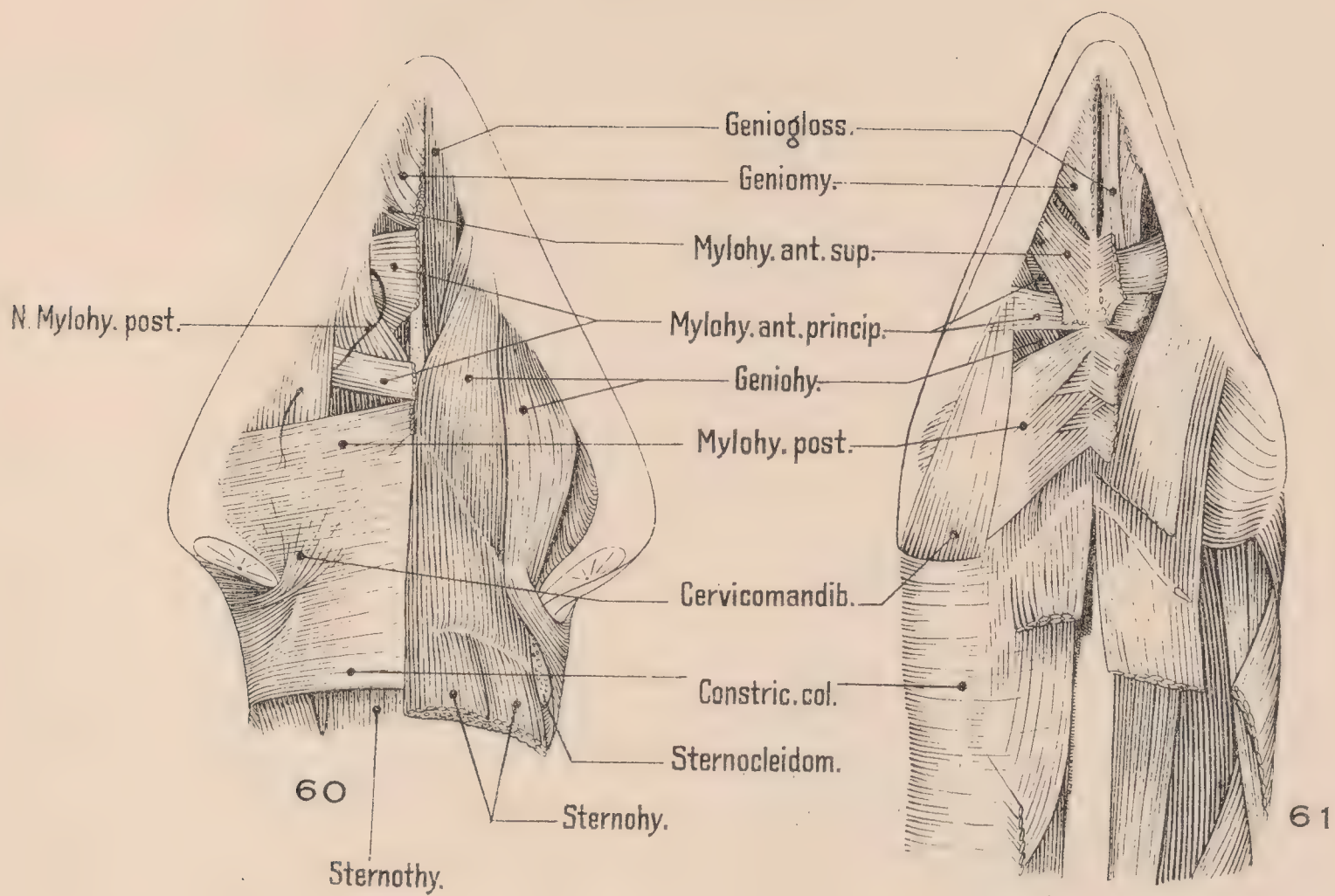
Fig. 59. *Gerrhonotus scincicauda webbi*,  $\times 1.8$ , A. M. N. H. No. 9159.

Fig. 60. *Xenosaurus grandis*,  $\times 1.8$ , A. M. N. H. No. 19381.

Fig. 61. *Anniella pulchra nigra*,  $\times 4\frac{1}{2}$ , A. M. N. H. No. 20426.

For abbreviations see p. 448.







Figs. 62, 63. COMPARISON OF SUPERFICIAL BODY MUSCULATURE OF AN ASCALATBOID AND AN AUTARCHOGLOSSID; shows also pattern of throat musculature in the Gekkonidæ (cf. Figs. 42–47). The muscles of the shoulder girdle of a scincomorph, *Gerrhosaurus*, a lizard with a cruciform interclavicle and perforated clavicle, are drawn for comparison with those of an anguimorph, *Xenosaurus* (Figs. 64–65), a form with T-shaped interclavicle and simple clavicles.

Fig. 62. *Gekko verticillatus*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 1812.

CERVICOMANDIB. = Cervicomandibularis. CONSTRIC. COL. = Constrictor colli. GENIOHY. LAT. = Geniohyoideus lateralis. GENIOHY. MED. = Geniohyoideus medialis. MYLOHY. ANT. = Mylohyoideus anterior. MYLOHY. POST. = Mylohyoideus posterior. PECT. = Pectoralis. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS PROF. = Rectus profundus. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoideus. STERNOHY. = Sternothyreoides.

Fig. 63. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 1721.

CLAVODELT. = Clavodeltoideus. COR. BRACH. LONG. = Coracobrachialis longus. RECTUS LAT. = Rectus abdominis lateralis. SCAP. HUM. ANT. = Scapulohumeralis anterior. Other abbreviations as in Fig. 62.



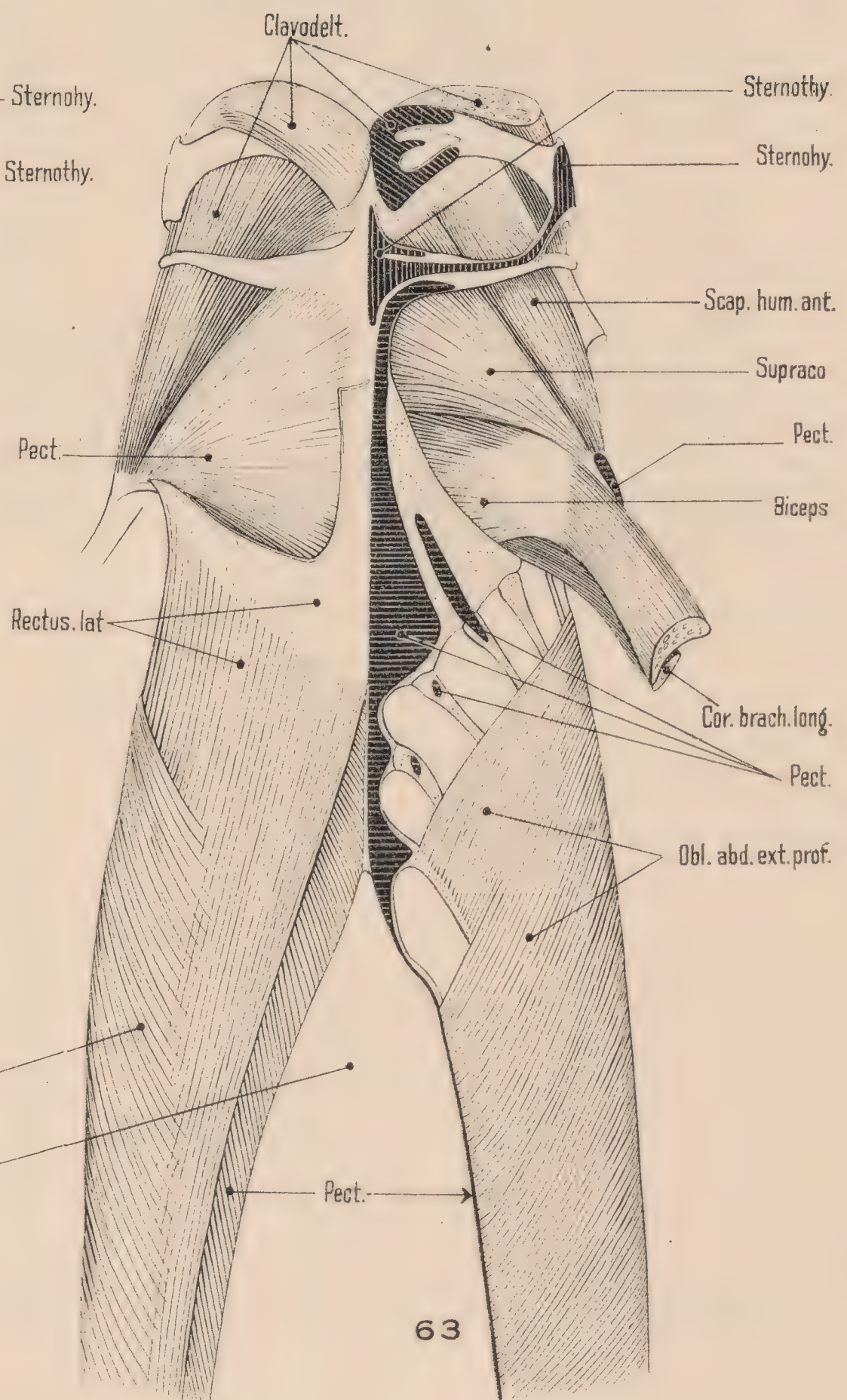
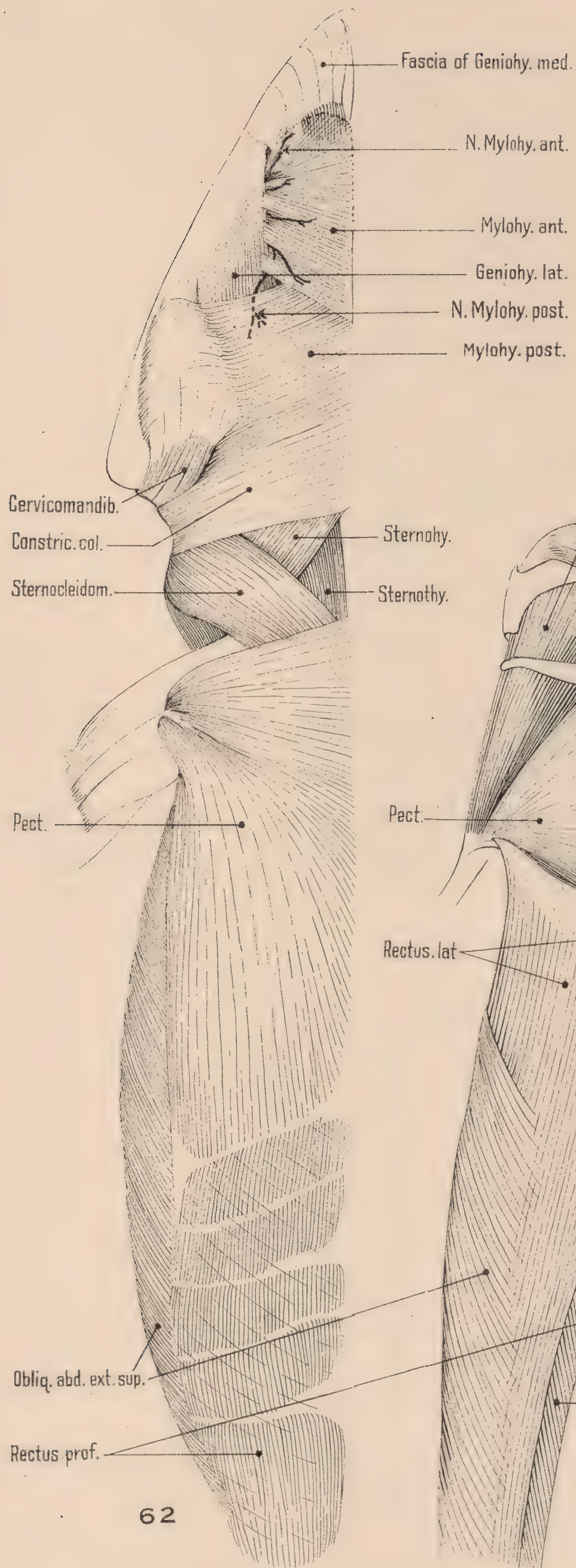


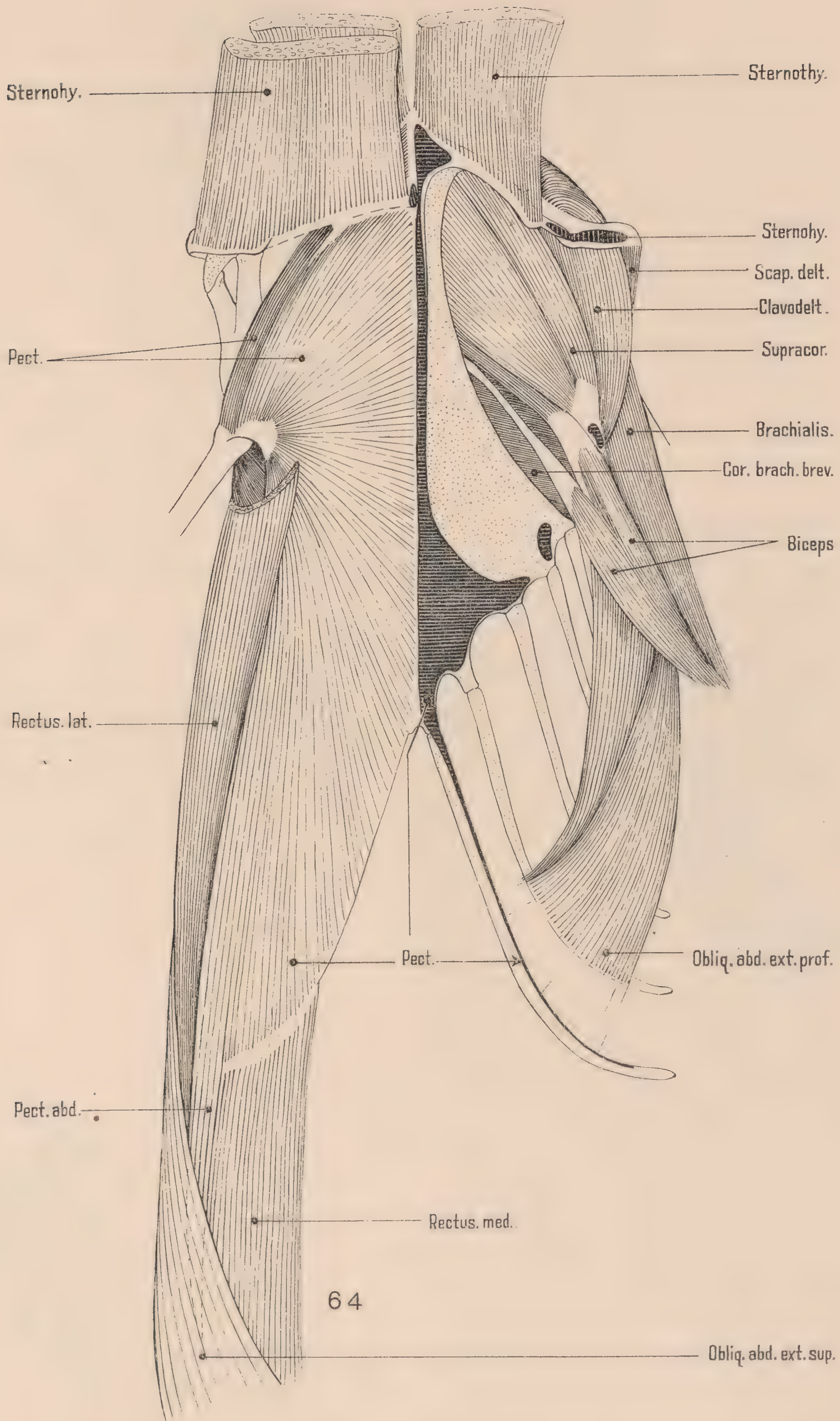


Fig. 64. Ventral shoulder and body muscles surrounding the shoulder girdle in the anguimorph *Xenosaurus*. Compare with Figs. 63 and 65-67.

*Xenosaurus grandis*,  $\times 4\frac{3}{4}$ , A. M. N. H. No. 19381.

CLAVODELT. = Clavodeltoideus. COR. BRACH. BREVUS. = Coracobrachialis brevis. OBLIQ. ABD. EXT. PROF. = Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. PECT. = Pectoralis anterior. PECT. ABD. = Pectoralis abdominis. RECT. MED. = Rectus abdominis medialis. RECT. LAT. = Rectus abdominis lateralis. SCAP. DELT. = Scapulodeltoideus. STERNOHY. = Sternohyoideus. STERNOTHY. = Sternothyreoideus. SUPRACOR. = Supracoracoideus.







Figs. 65-66. VENTRAL SHOULDER MUSCULATURE IN *Gerrhosaurus* AND *Xenosaurus* to show the relations of the muscles to the excavated parts and the processes of the bony elements. Compare with Figs. 63 and 64.

Fig. 65. *Xenosaurus grandis*,  $\times 3\frac{7}{8}$ , A. M. N. H. No. 1938.

COR. BRACH. LONG. = Coracobrachialis longus. SCAP. HUM. ANT. = Scapulohumeralis anterior. SUPRACOR. = Supracoracoideus. Other abbreviations as in Fig. 64.

Fig. 66. *Gerrhosaurus zechi*,  $\times 1\frac{1}{2}$ , A. M. N. H. No. 10721.

SCAP. HUM. POST. = Scapulohumeralis posterior. Other abbreviations as in Figs. 64 and 65.

Fig. 67. CORACOID OF *Gerrhosaurus*,  $\times 1\frac{1}{2}$ , showing relations of muscle insertions to the coracoideal fenestræ.

LAT. COR. FEN. = Lateral (1'') coracoidal fenestra. MED. COR. FEN. = Median (2'') coracoidal fenestra.



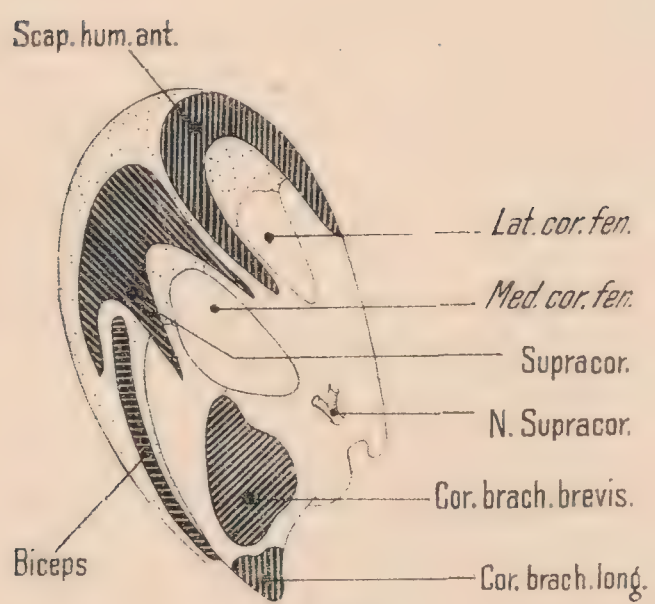
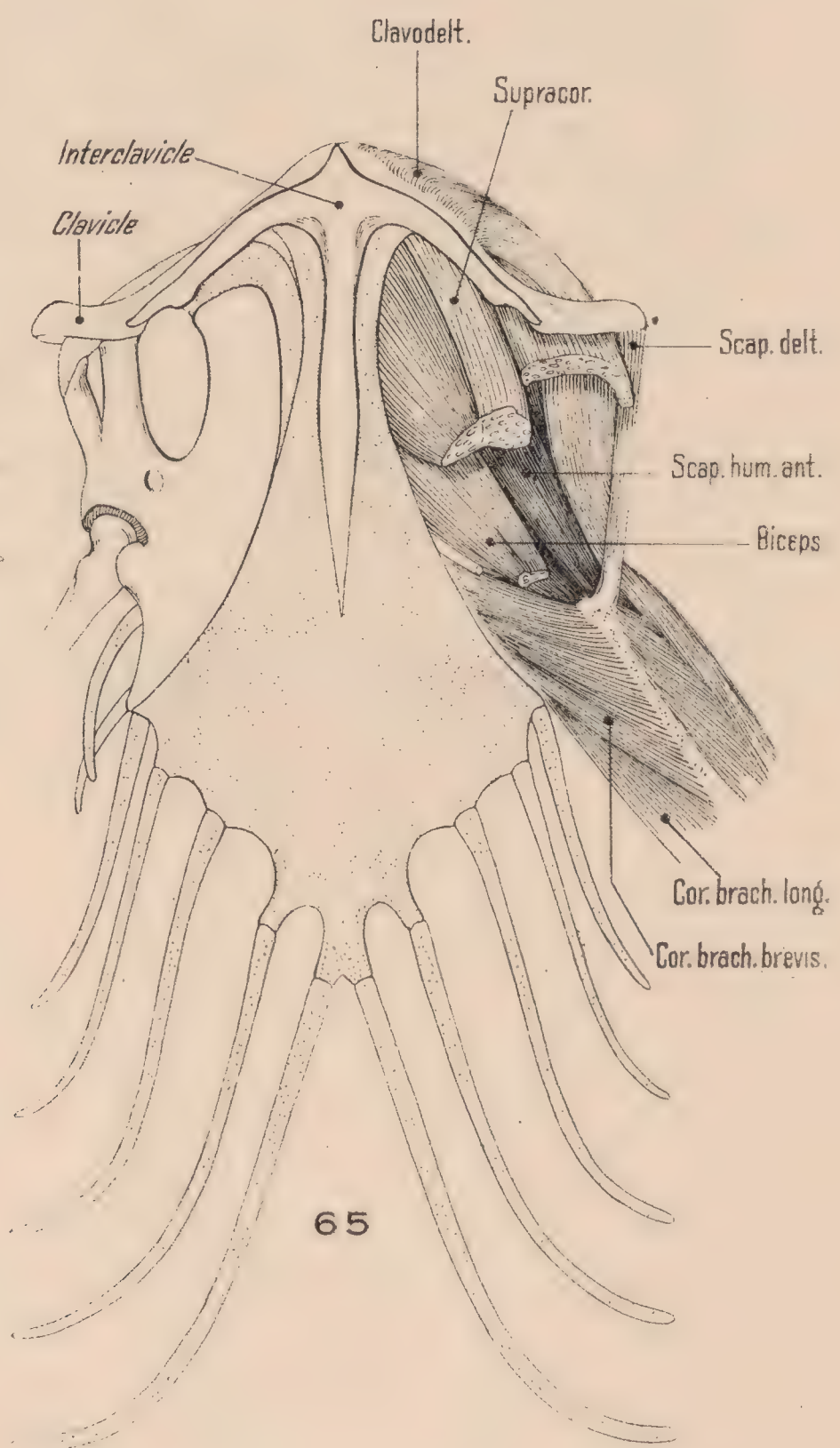
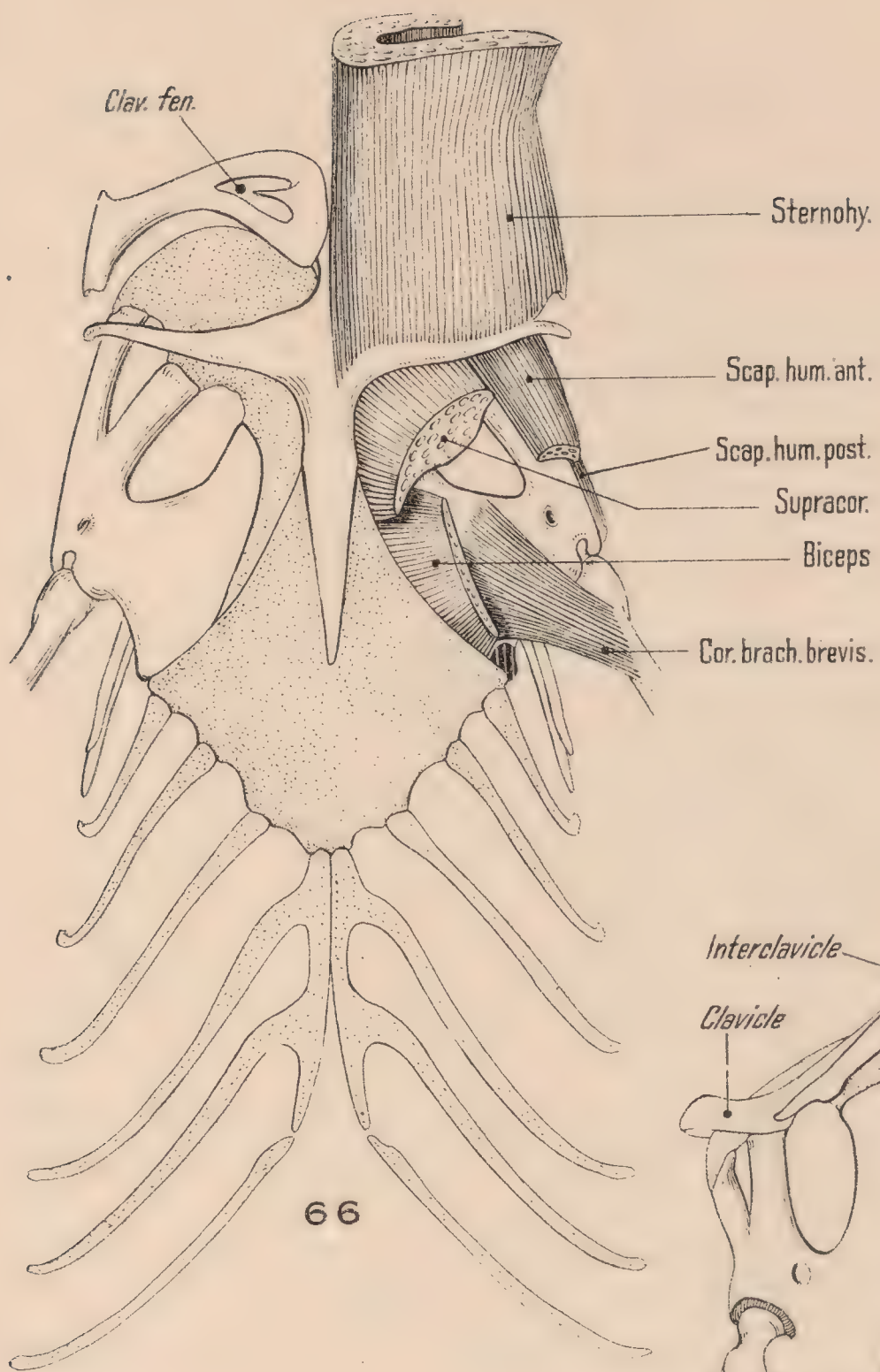




Fig. 68. Shoulder girdle and parasternum of the degenerate teiid, *Bachia intermedia*,  $\times 14$ . Bones and cartilages are drawn from a specimen, A. M. N. H. No. 22731, prepared by Dr. G. K. Noble. Muscles are added from a dissection of A. M. N. H. No. 22730. Ventral view. Four segments omitted in the mid-dorsal region.

The clavicles retain the hook-shaped form characteristic of teiids. The cartilage closing the scapulocoracoid fenestra anteriorly is reduced to a ligament. The sternum is greatly reduced, and contains a large fontanelle.

The xiphisternum is asymmetrical and shows its serial homology with the parasternum by the circumstance that the anterior parasternal wing on the right side has developed into a xiphisternal rod (P).

The parasternum is greatly specialized in connection with body muscles used in terrestrial locomotion and has no union with the rib at its posterior end on the right side.

The segmentation of the skin corresponds with the metamerism of the body.

Fig. 68a. Left forefoot of A. M. N. H. No. 22731,  $\times 16\frac{1}{2}$ .

The carpals are reduced to five. The last metacarpal (IV) is cartilaginous, the fifth is absent.

PALM. SES. = Palmar sesamoids. OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS PROF. = Rectus profundus. RECTUS SUP. = Rectus superficialis (= Rectus lateralis + Rectus medianus) closely joined to skin, along with the wings of the parasternum.



Clavicle

Interclavicle

Sternum

Xiphisternum

Parasternum

Obliq. abd. ext. sup.

Scalares.

IV

Palm. ses.

IV

U.

R.

Centrale

68 *a*

Rectus prof.

Skin segments

Rectus sup.

68

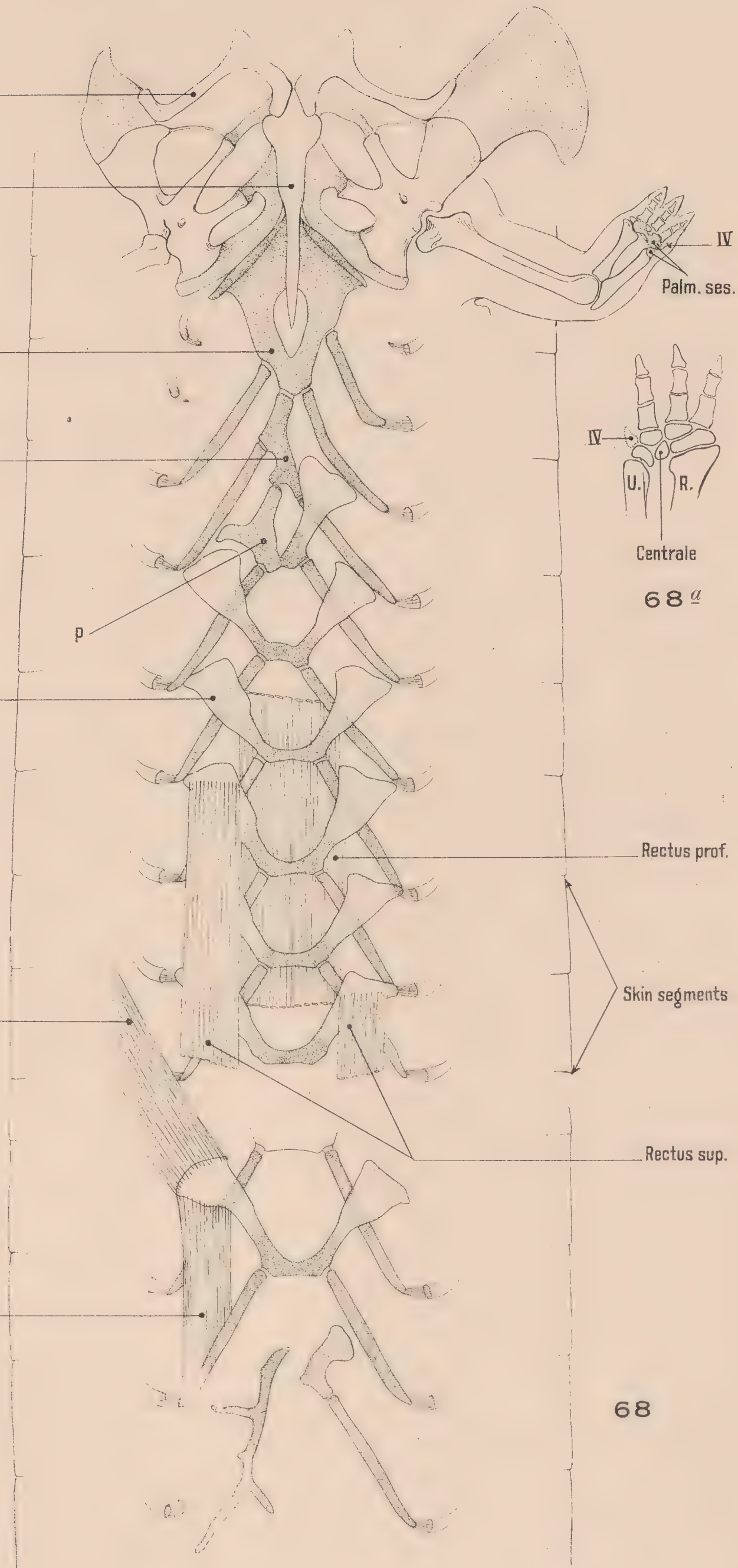




Fig. 69. Shoulder girdle of *Xantusia vigilis*,  $\times 15$ , A. M. N. H. No. 9204, prepared by Dr. G. K. Noble. The interclavicle is cruciform and the clavicles are perforate. There are two small sternal fontanelles. The supracoracoid foramen is enormous. The formula of the scapulo-coracoidal fenestræ is OXXO.



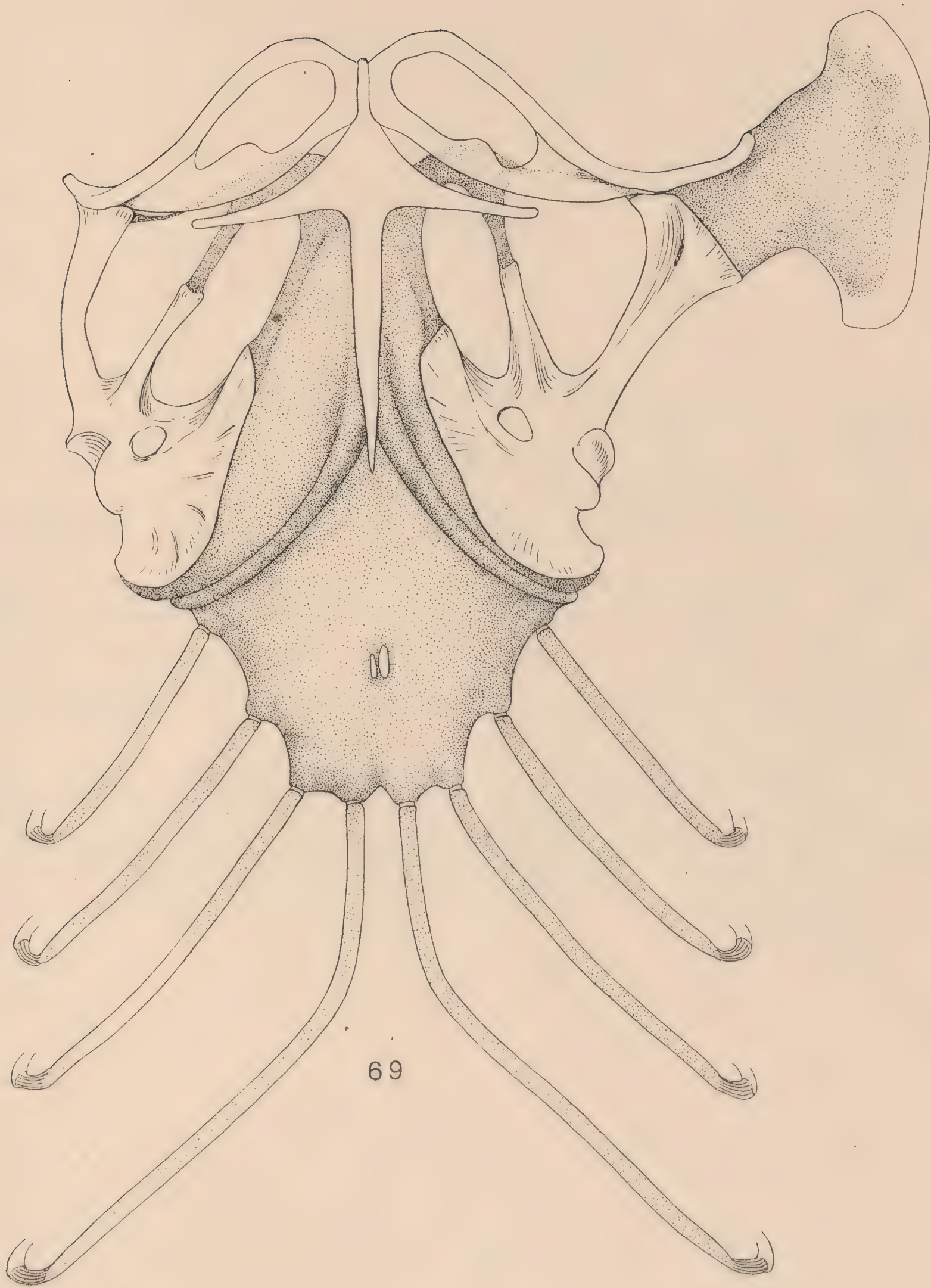




Fig. 70. Cartilaginous shoulder girdle of the degenerate anguroid, *Anniella pulchra nigra*,  $\times 10$ , A. M. N. H. No. 20426, left clavicle from the side.

Fig. 71. Both clavicles, direct ventral view of the same.

Fig. 72. Muscles adjoining the shoulder girdle of the same.

OBLIQ. ABD. EXT. SUP. = Obliquus abdominis externus superficialis. RECTUS SUP. = Rectus superficialis. STERNOCLEIDOM. = Sternocleidomastoideus. STERNOHY. = Sternohyoideus. STERNOTHY. = Sternothyreodeus.

Fig. 73. Shoulder girdle of the degenerate scincoid, *Feylinia currorii*,  $\times 10$ , after Rabanus (1906-1915, Pl. XXIII, fig. 33). The clavicles are disappearing, the scapulocoracoid remains. The sternum is reduced to a small median parasternal-like cartilage (cf. Fig. 75).

Fig. 74. Right half of the pelvis of a degenerate teiid, *Bachia intermedia*,  $\times 22$  (same specimen as Fig. 68a).

The hind limbs in the teiids and amphisbænids tend to disappear more rapidly than the forelimbs. In this example, the ilium is fused with the ischium, the pubis and epipubis are separate, the femur is relatively large, the tibia and fibula are much reduced, and the hind foot is represented by a single bone, probably the fibulare.



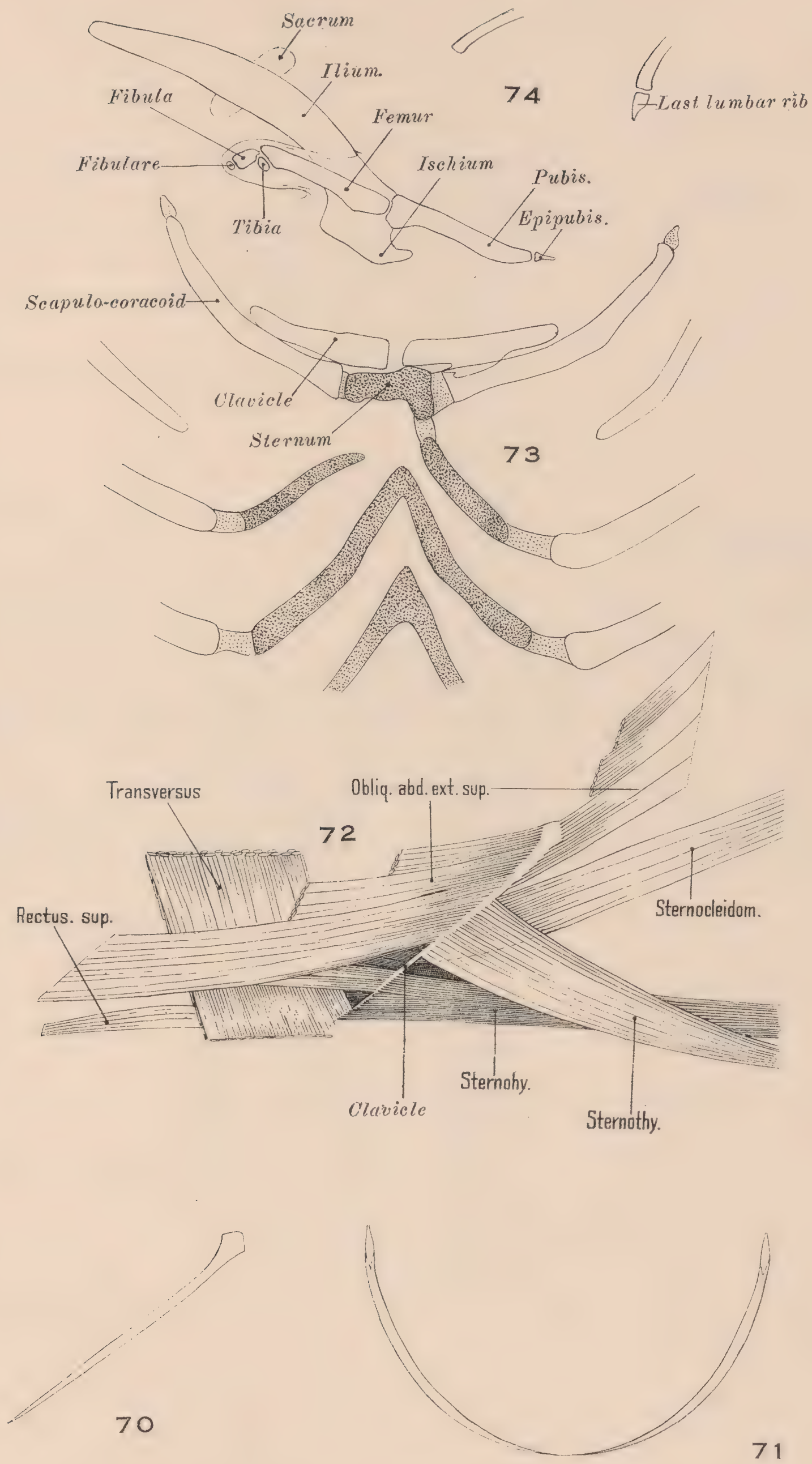




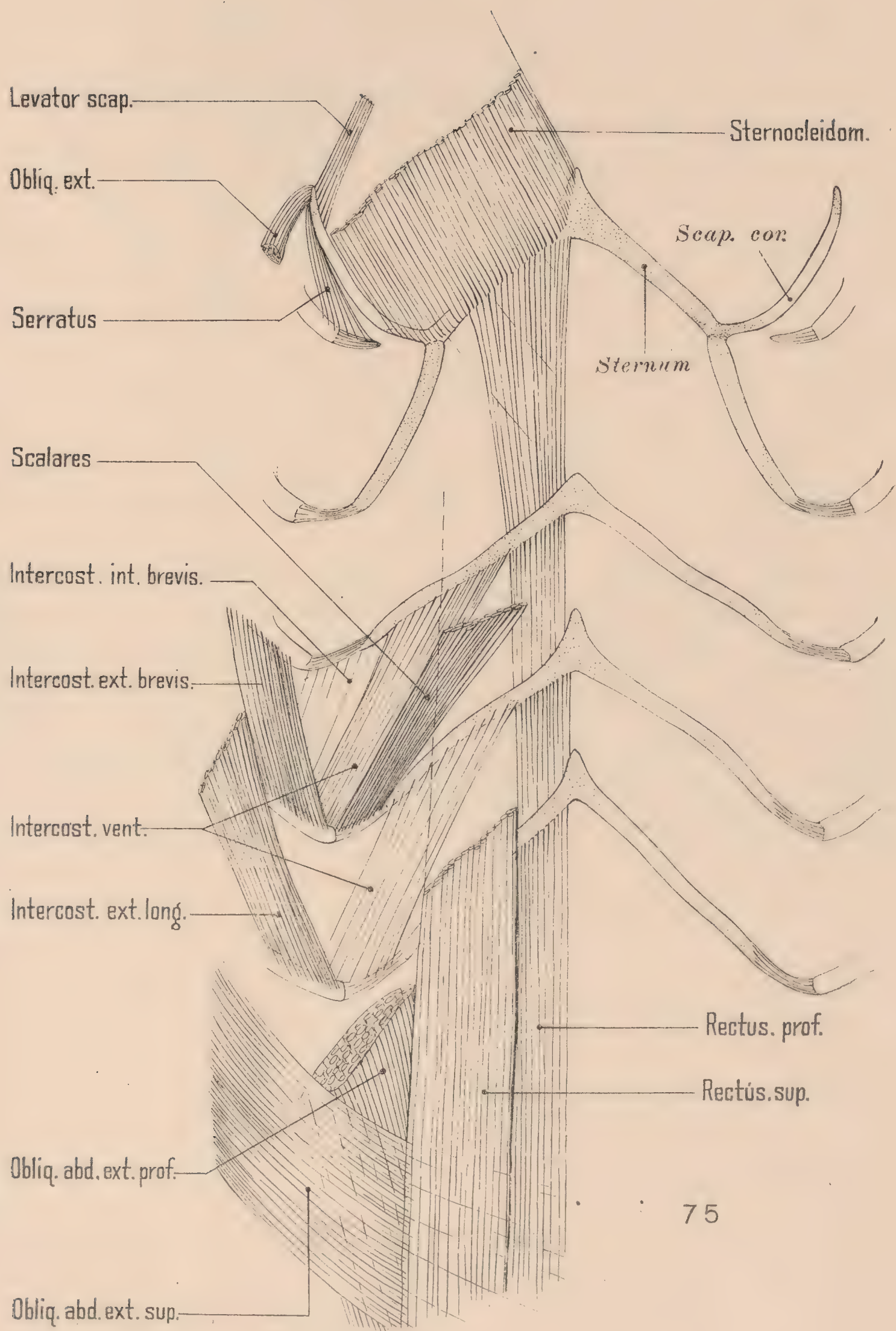
Fig. 75. Shoulder girdle of the degenerate scincoid, *Dibamus novæ-guinææ*,  $\times 22$ , A. M. N. H. No. 1264.

The scapulocoracoids are small, partly bony, and connected to the tip of the first dorsal rib by a muscle which probably represents the Serratus. The sternum has almost the exact shape of the parasternal chevrons which succeed it. The Rectus profundus lies dorsal to the parasternum and the Rectus superficialis lies ventral to it in the usual way. The posterior parasternal chevrons are omitted.

The Transversus is present but is not shown. The Scalares join the skin on each alternate segment with the Rectus superficialis.

INTERCOST. EXT. BREVIS=Intercostalis externus brevis. INTERCOST. EXT. long.=Intercostalis externus longus. INTERCOST. INT. BREVIS.=Intercostalis internus brevis. OBLIQ. ABD. EXT. PROF.=Obliquus abdominis externus profundus. OBLIQ. ABD. EXT. SUP.=Obliquus abdominis externus superficialis. RECTUS PROF.=Rectus profundus. RECTUS SUP.=Rectus superficialis. SCAP. COR.=Scapulocoracoid.







Figs. 76–81. A SERIES SHOWING MODIFICATIONS OF THE CLAVICLE IN VARIOUS LIZARDS (cf. Figs. 62–75). Ventral views, left clavicle.

Fig. 76. Interclavicle and end of left clavicle of *Proterosaurus speneri*, after Credner (1888, Fig. 19, p. 520).

Fig. 77. *Aræoscelis*,  $\times 2\frac{1}{4}$ , after Williston (1914, Fig. 4, L).

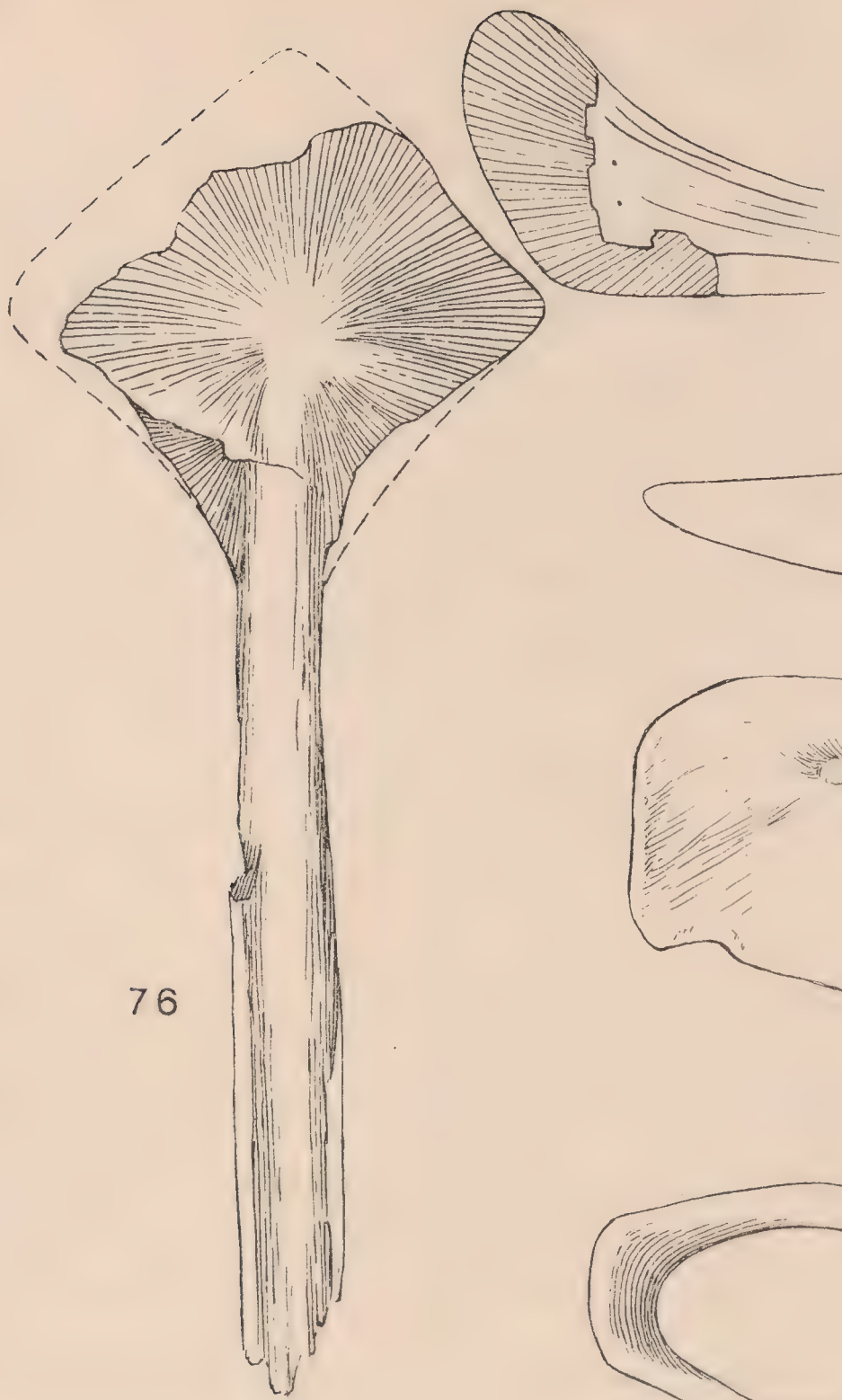
Fig. 78. *Trachysaurus rugosus*,  $\times 3$ , Skel. in Dept. Herpetol., A. M. N. H.

Fig. 79. *Lacerta simonyi*,  $\times 4\frac{1}{2}$ , after Sibenrock (1894, Pl. iv, fig. 24).

Fig. 80. *Lacerta serpa*, after Krieg (1919, Fig. 1, p. 574).

Fig. 81. *Zonurus giganteus*,  $\times 3$ , Skel. in Dept. Herpetol., A. M. N. H.





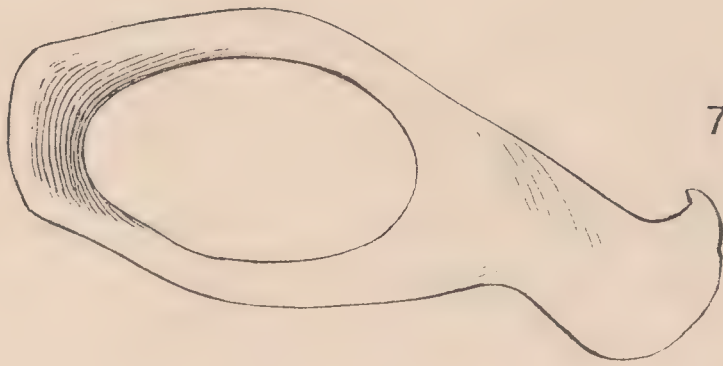
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Figs. 82-98. OSTEODERMS OF LIZARDS. Figs. 84-89, Scincomorpha. Figs. 90-98, Anguimorpha.

The osteoderms are on a higher plane of development in the Anguimorpha than in the Scincomorpha. The ventral scutes of the Anguimorpha appear never to be compound; those of Scincomorpha are always so. Some approach to geckonoid conditions (Fig. 83) is seen in the scincs (Fig. 84). The least developed scutes of the Anguimorpha (Figs. 90 and 92) show a slight advance upon the most specialized scutes of the Scincomorpha (Figs. 87 and 89). The most highly specialized scutes are those of the Glyptosauridæ and Helodermatidæ (Figs. 94-98). The least specialized are apparently the diffuse scutes of the cotylosaur, *Pantylus*, and of the gecko, *Tarentola* (Figs. 82-83). The position of the horny scales covering the scutes is indicated in many of the figures.

Fig. 82. *Pantylus*,  $\times 2$ , after Williston (1916a, Fig. 30, p. 175).

Fig. 83. *Tarentola mauritanica*, ventral scales and scutes, after Otto (1909, text-fig. 19, p. 234).

Fig. 84. *Scincus officinalis*, scute from right side of cloaca, after Otto, (1909, text-fig. 5, p. 210).

Fig. 85. *Gongylus* [*Chalcides*] *ocellatus*, scute from dorsal surface of tail, after Otto (1909, text-fig. 9, p. 218).

Fig. 86. *Scincus officinalis*, scute from the cervical region, after Otto (1909, text-fig. 4, p. 209).

Fig. 87. *Lygosoma tenue*, scute from the cervical region, after Otto (1909, text-fig. 13, p. 225).

Figs. 88-89. *Gerrhosaurus nigrolineatus*, after Schmidt (1913a, Figs. D=88, ventral, C=89, dorsal, p. 80),  $\times 3$ .

Figs. 89a and b. *Zonosaurus madagascariensis*,  $\times 10$ , after Schmidt (1913a, Figs. M<sub>2</sub> dorsal, M<sub>3</sub> ventral).

Fig. 90. *Zonurus cordylus*, mid-dorsal scute and scale, after Otto (1909, text-fig. 1, p. 204).

Fig. 91. *Zonurus cordylus*, mid-dorsal scute, after Otto (1909, Pl. ix, fig. 1).

Fig. 92. *Anguis fragilis*, mid-dorsal scute, after Otto (1909, text-fig. 2, p. 207).

Fig. 93. *Gerrhonotus liocephalus*, dorsal scute,  $\times 8$ , after Schmidt (1914, Pl. vi, fig. 68).

Fig. 94. *Xestops*, scute from the body,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5175.

Fig. 95. *Glyptosaurus*, scute from the body,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5113, Bridger Eocene.

Fig. 96. *Glyptosaurus*, scute from the head,  $\times 1\frac{1}{4}$ , Dept. Vert. Pal., A. M. N. H. No. 5109.

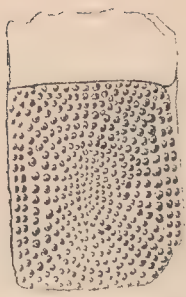
Fig. 97. *Placosaurus rugosus*, scute from the head,  $\times .8$  after Gervais (1859, Atlas, Pl. LXIV, fig. 2a).

Fig. 98. *Heloderma horridum*,  $\times 4$ , A. M. N. H. No. 7216.

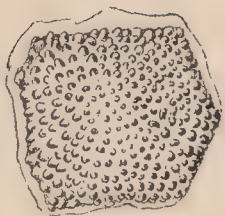




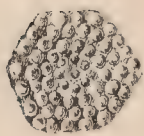
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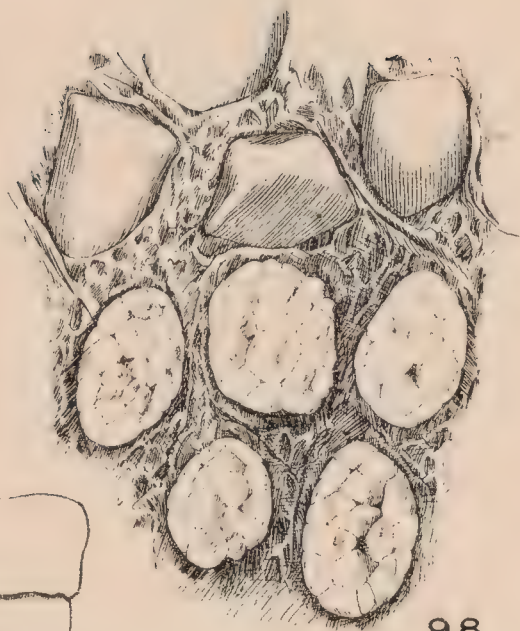
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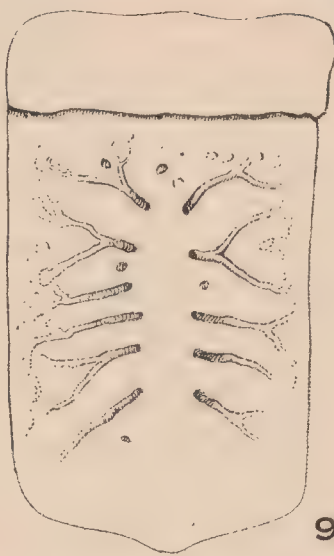
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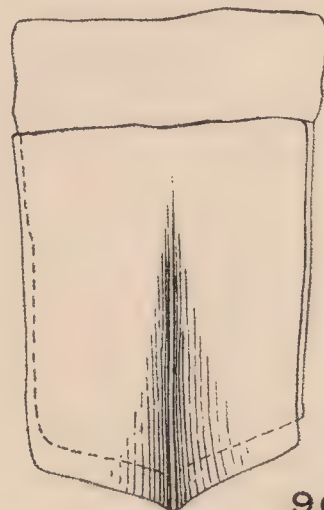
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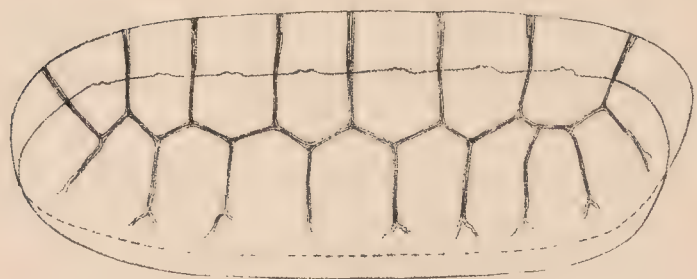
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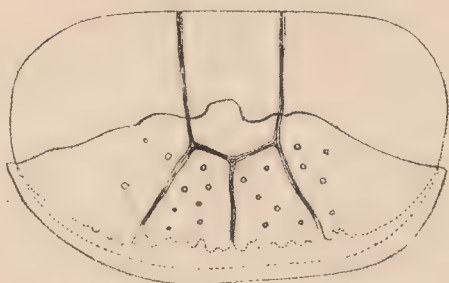
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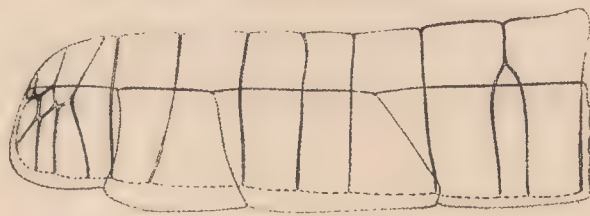
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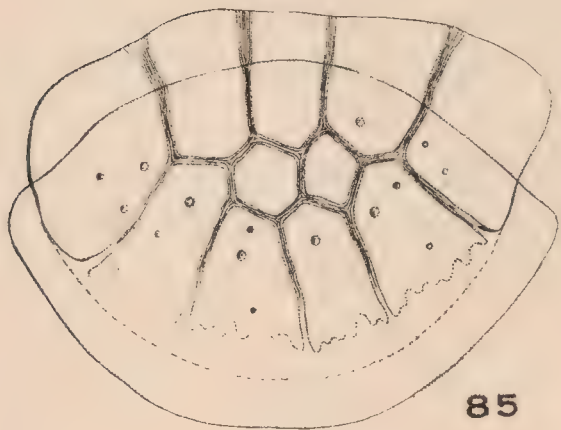
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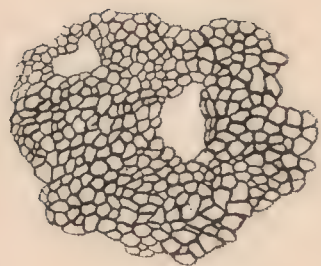
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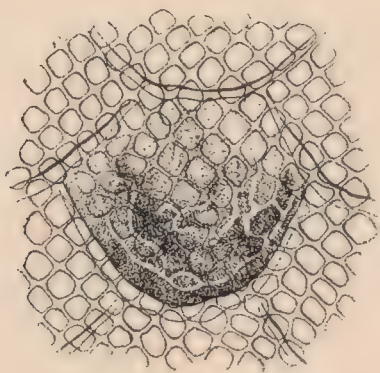
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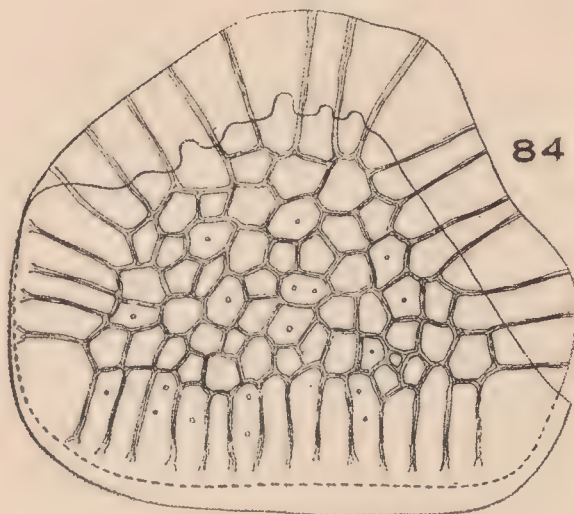
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Figs. 99–105. SKULLS AND VERTEBRÆ OF GLYPTOSAURIDÆ, AND VERTEBRÆ OF OTHER ANGUIIDS.

Fig. 99. First caudal vertebra of *Gerrhonotus scincicauda scincicauda*,  $\times 6\frac{1}{2}$  A. M. N. H. No. 595. The transverse processes arise from the whole length of the centrum as in the Glyptosauridæ. The chevrons are attached intercentrally at C.

Fig. 100. First caudal vertebra of *Heloderma* sp.?,  $\times 3\frac{1}{2}$ , Skel. in Dept. Comp. Anat., A. M. N. H. The transverse processes arise from the anterior two-thirds of the centrum. The chevrons are attached intercentrally at C.

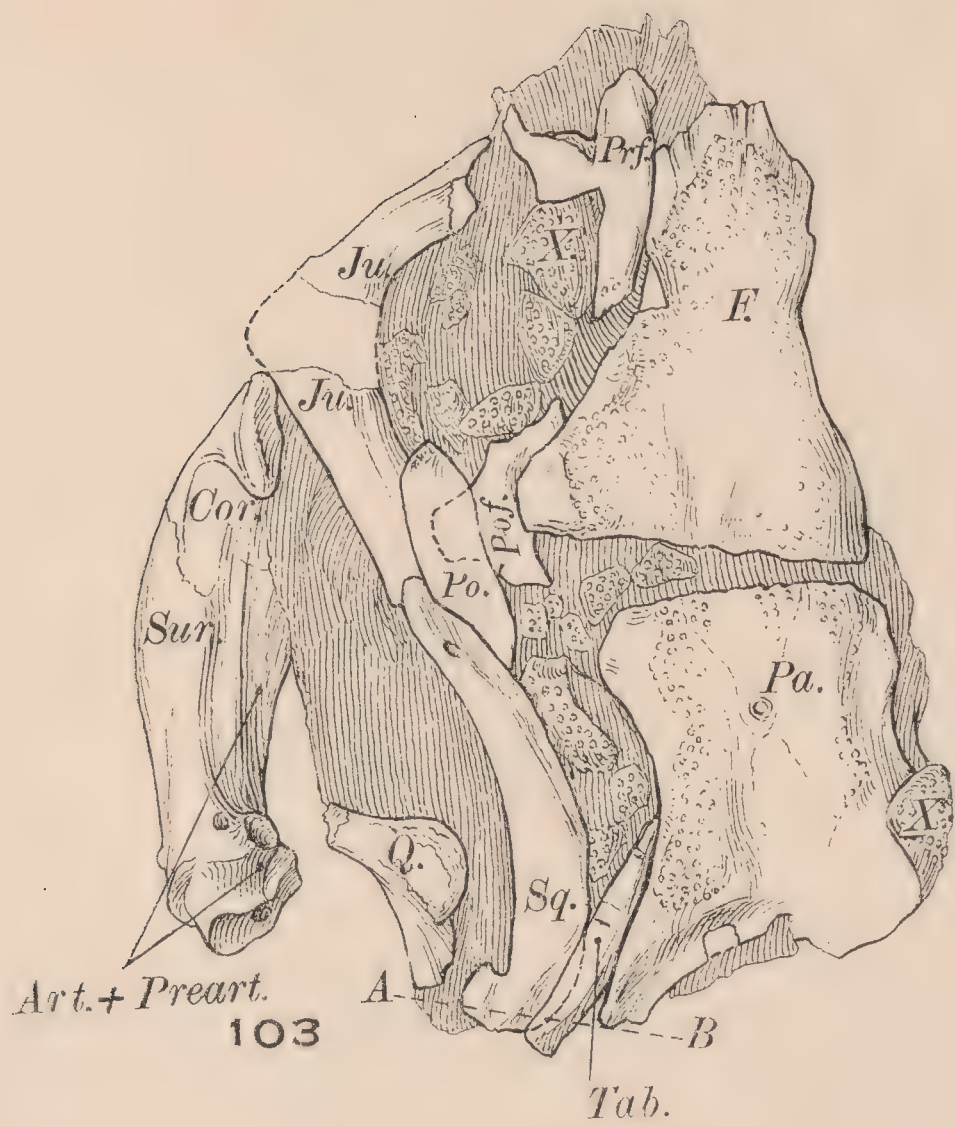
Fig. 101. *Xestops*, Dept. Vert. Pal., A. M. N. H. No. 5175. The transverse processes arise from the whole length of the centrum as in *Gerrhonotus*. The chevrons are attached centrally at C.

Fig. 102. *Xestops*,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5175. Mid-dorsal vertebra, ventral view for comparison with Figs. 15, 20, and 21.

Fig. 103. Skull of *Xestops*,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5168. Dorsal view. The skull is crushed flat. The disarticulated bones lie nearly in position showing the correct relation of the Frontals (*F.*), Parietals (*Pa.*), Prefrontal (*Prf.*), Postfrontal (*Pof.*), Postorbital (*Po.*), Jugal (*Ju.*), Squamosal (*Sq.*), Quadrate (*Q.*), and the posterior end of the lower jaw. (Cf. Figs. 106–110.)

Figs. 104–105. *Placosaurus rugosus*. Top of skull of type specimen showing same kind of osteoderms (Figs. 104–105) as in *Glyptosaurus* and on the side of the head in *Xestops* (Fig. 103, X), after Gervais (1859, Atlas, Pl. LXIV, figs. 2–2a).



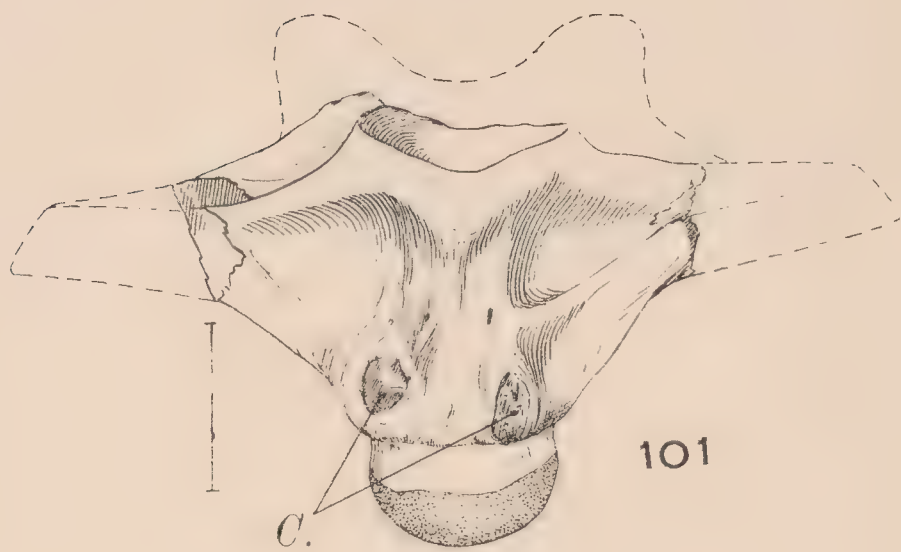
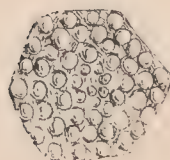


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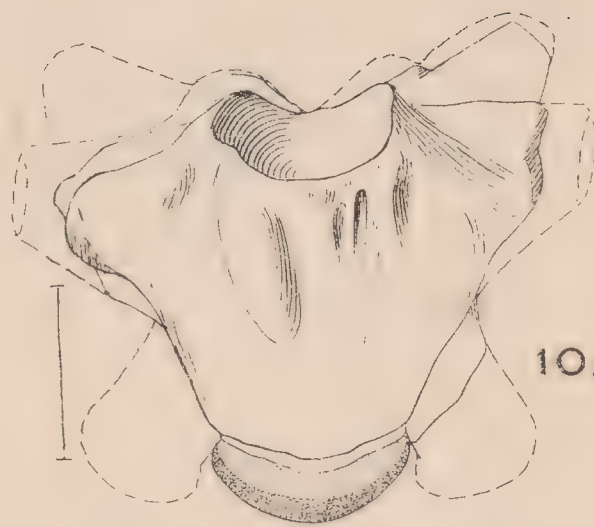
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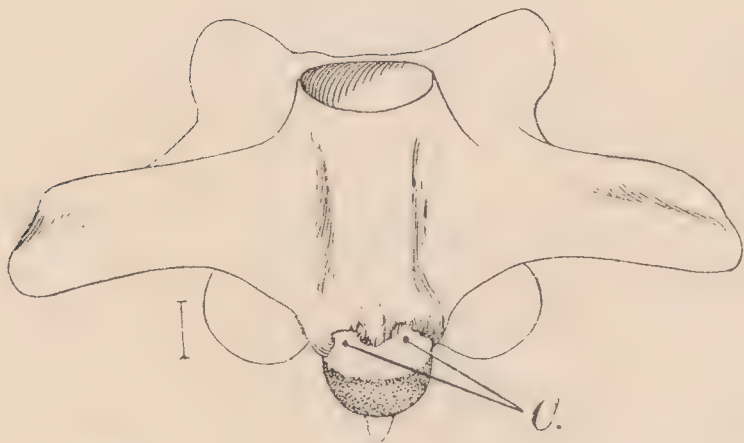
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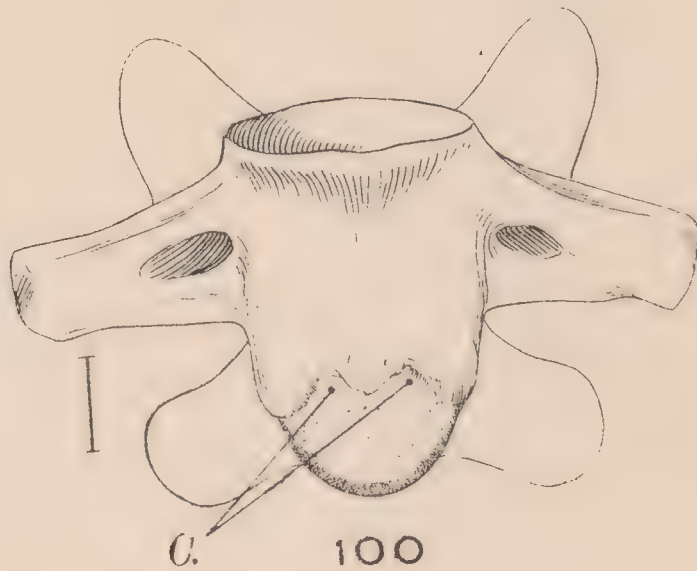
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Figs. 106, 107. RECONSTRUCTION OF SKULL OF *Xestops*, based chiefly on specimens figured in Fig. 103. The shape of other bones is seen on the following specimens: Dept. Vert. Pal., A. M. N. H. No. 5113, prefrontal, lacrymal<sup>1</sup>; A. M. N. H. No. 5175, jugal, maxillaries, premaxillary, tooth row, and occiput; A. M. N. H. No. 5176, sutures in lower jaw (cf. Fig. 112). A superciliary bone was probably present but has not been recognized in our material. Comparison should be made with a figure of *Glyptosaurus* by Douglass (1908).

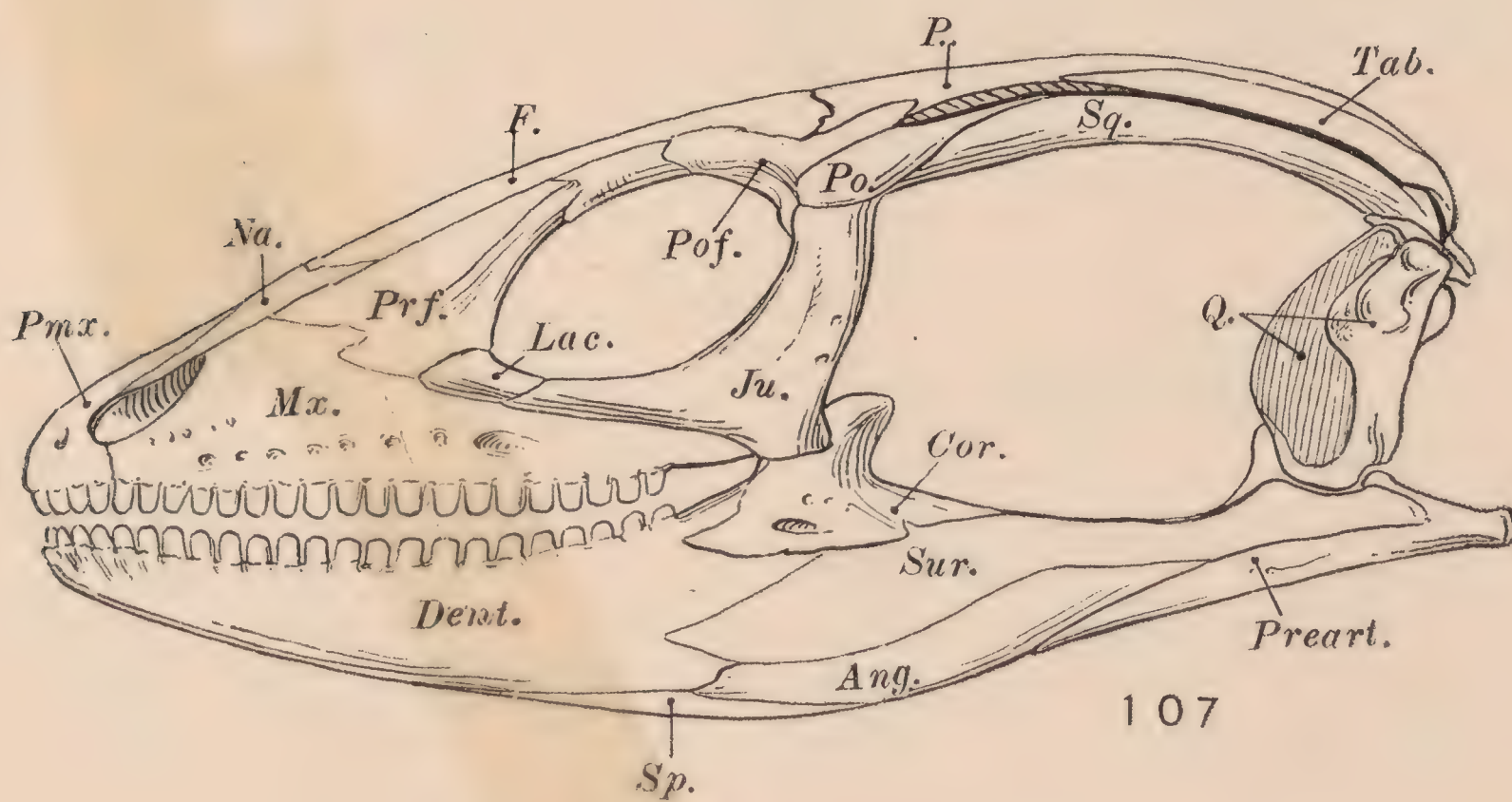
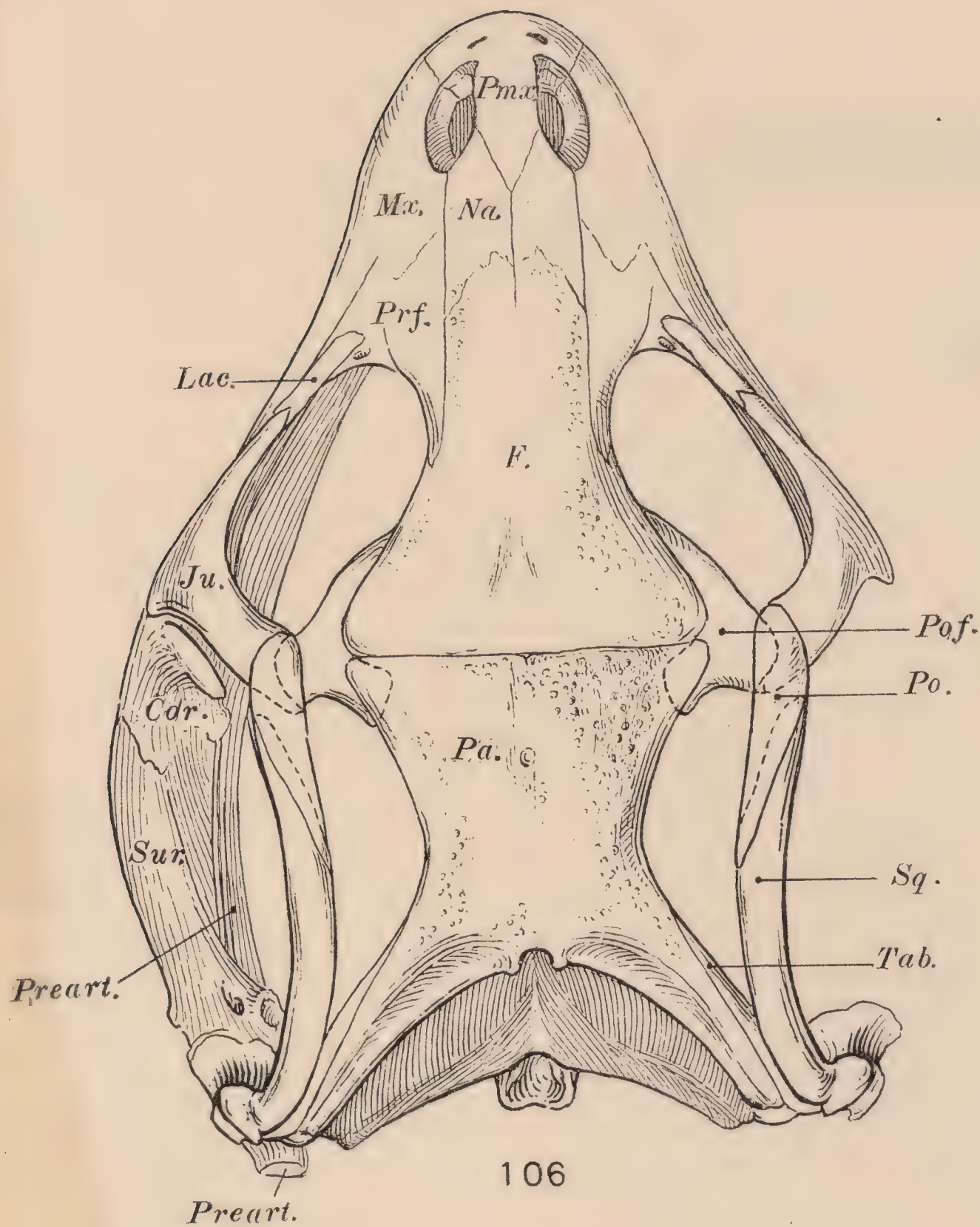
Fig. 106. Dorsal view,  $\times 1.2$ .

Fig. 107. Lateral view,  $\times 1.2$ .

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<sup>1</sup>Presence indicated by a groove in the prefrontal.







Figs. 108-112. SKULL OF THE ANGUID, *Gerrhonotus*, AND PORTIONS OF SKULLS OF GLYPTOSAURIDÆ, for comparison with Figs. 106, 107.

Fig. 108. Top of skull of *Gerrhonotus scincicauda scincicauda*,  $\times 2$ , A. M. N. H. No. 595. Superciliare omitted. General similarities to *Xestops* are shown. The heavy secondary covering of bony scales is preserved on the right side.

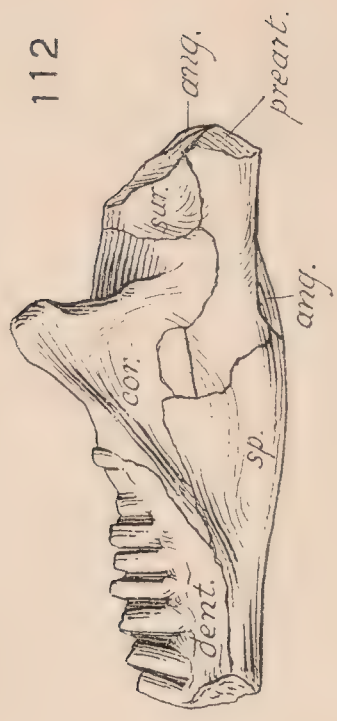
Fig. 109. Section of quadrato-parietal region of *Xestops* through line A-B, Fig. 103,  $\times 3$ . The squamosal has a basal expansion resting upon the head of the quadrate. The paroccipital is separate from the exoccipital and its posterior extremity (*Parocc.*) lies beneath the tabular-parietal suture. The exoccipital bears a dorsal groove for the reception of the tabulare. There is a muscular excavation on the posterior border of the parietal. The quadrate is rotated out of position due to crushing.

Fig. 110. Postero-internal view of quadrate of same specimen as Fig. 109,  $\times 3$ . The broadened internal "wing" is represented in *Heloderma* by a slight ridge and is absent in *Gerrhonotus*.

Fig. 111. Anterior portion of lower left dentary, internal view of *Xestops*,  $\times 2\frac{1}{2}$ . Dept. Vert. Pal., A. M. N. H. No. 5175. The direction of the teeth at the symphysis, the highly pleurodont character of the semi-solid teeth, and the wrinkling of the blunt crowns are shown. The teeth are firmly attached to the dentary for nearly their whole length.

Fig. 112. Sutures on internal face of middle of lower jaw of a glyptosaurid,  $\times 1$ , Dept. Vert. Pal., A. M. N. H. No. 5176, Wasatch Eocene. The Meckelian sulcus is closed. The splenial is large. The elements are all suturally distinct.

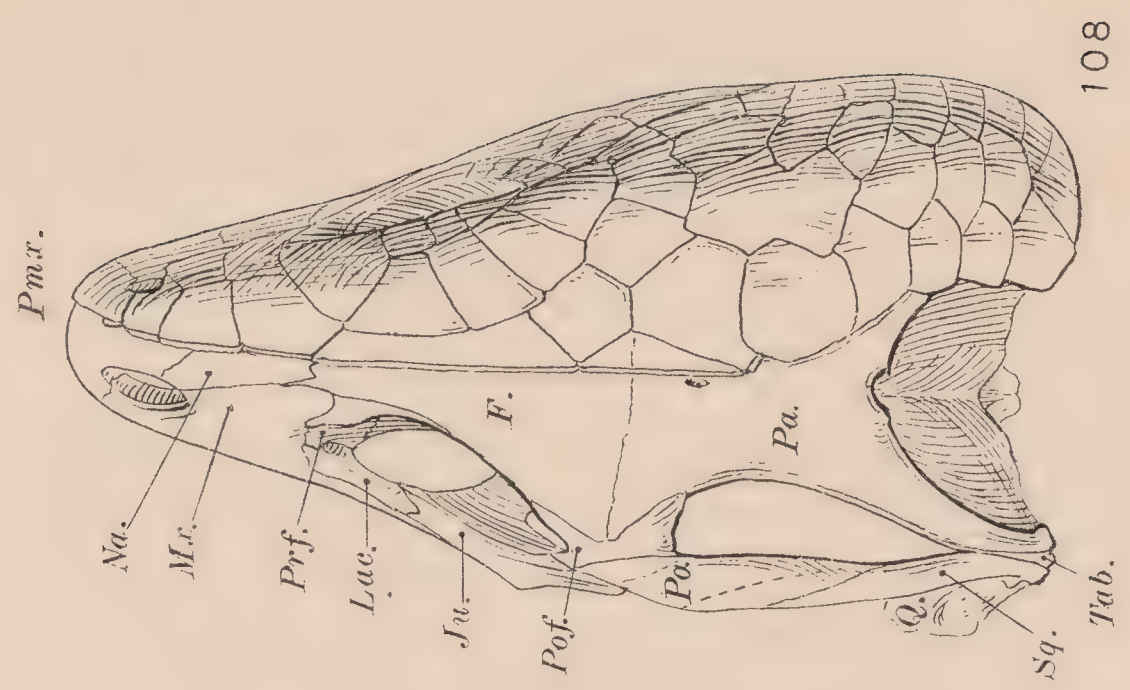




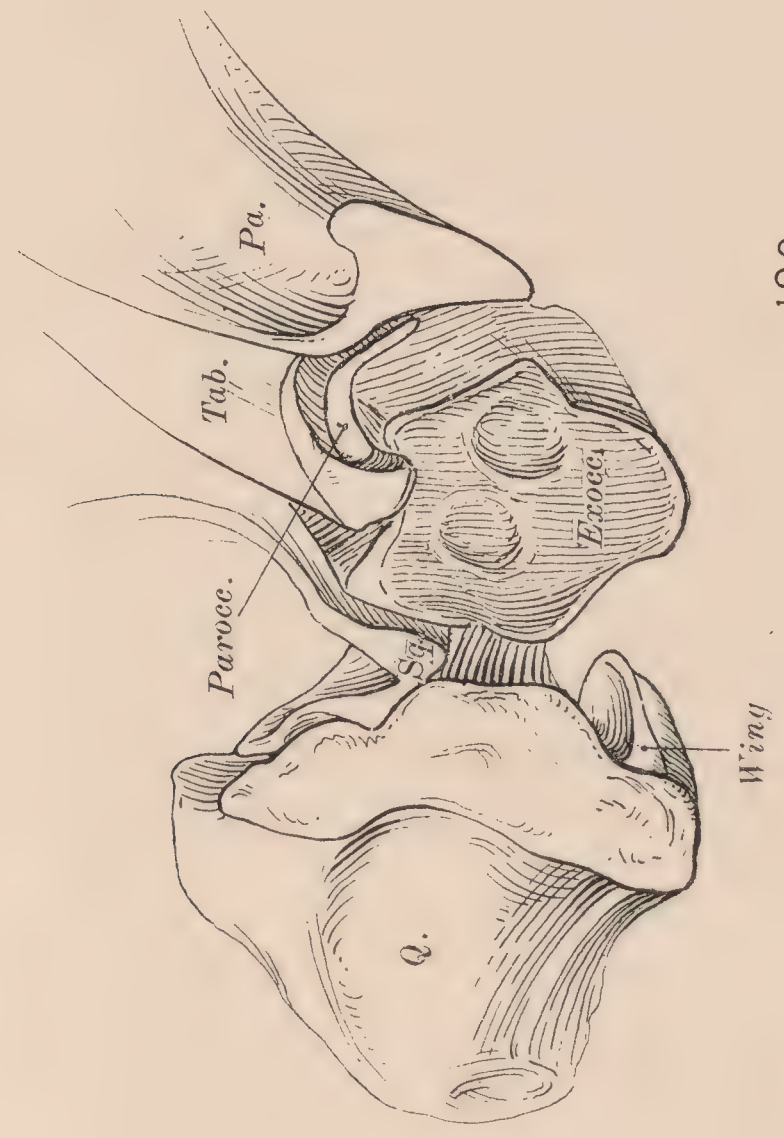
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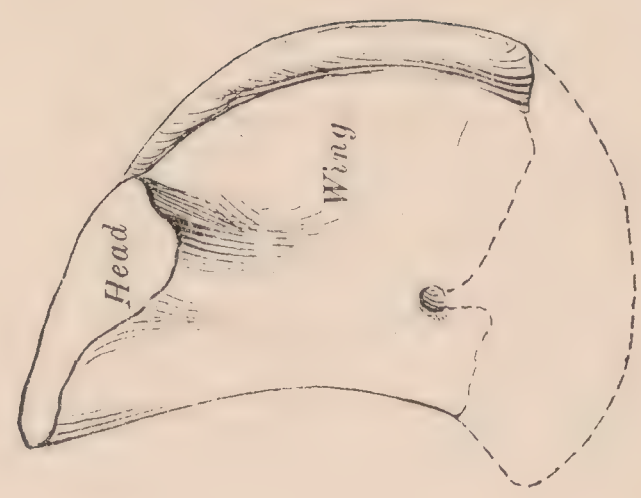
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## Article XII.—AVIAN FOSSILS FROM THE MIOCENE AND PLIOCENE OF NEBRASKA

BY ALEXANDER WETMORE

### INTRODUCTION

Field work in the fossil deposits of Sioux County, northwestern Nebraska, by parties sent out from The American Museum of Natural History has yielded small numbers of fossil bones of birds that until the present time have remained unstudied. Through the kind offices of Dr. W. D. Matthew, Curator of Vertebrate Palæontology, this material came into my hands for examination, while at the same time, through the courtesy of Dr. W. J. Sinclair, I was enabled to see specimens secured by the Princeton University Expedition of 1914 from the same deposits. Mr. Harold J. Cook, of Agate, Nebraska, in addition has allowed me to study bones that he has collected personally from the same area. It has thus been possible to assemble a small series of fossil bones of birds from the beds in question, in all seventeen from the American Museum, three from Princeton University Museum, and three from the private collection of Mr. Harold J. Cook; not a large number, but one that permits of some insight into the avifauna of the periods represented. The collection is especially valuable since it is accompanied by full data as to site and location. To the gentlemen mentioned I wish to acknowledge my indebtedness for information and material. My thanks are due especially to Dr. Matthew through whose suggestion this work was undertaken.

### AGE OF DEPOSITS

The Snake Creek beds, from which come most of the specimens here studied, originally were considered as wholly Lower Pliocene but recently detailed study has led Dr. Matthew (to whom I am indebted for this information) to distinguish two phases in the fauna represented: first, a deposit that contains remains of *Hipparion* and *Pliohippus*, among other mammals, that is Lower Pliocene; and, second, a layer, apparently below the first, no less rich in fossils, that is thought to be Upper Miocene, as the species characteristic of the Pliocene are lacking.

Explorations in the summer of 1922 yielded a few more avian bones from the Lower Sheep Creek beds, in what Dr. Matthew considers as the earliest phase of the deposits containing *Merychippus*. This horizon is believed to be early Middle Miocene, older than Mascall.



A detailed description of the beds as a whole has been given by Matthew and Cook<sup>1</sup> from field work in 1908 when the desposits were first discovered. Additional information is included by Dr. Sinclair in a paper<sup>2</sup> drawn from work performed for the Princeton University Museum during the summer of 1914. The bird bones from these beds, though often broken, are well preserved; they vary from whitish to dark slate in color. Some show evidence of wear, while others are remarkable for the manner in which they have retained minute details of structure.

#### DISCUSSION OF THE AVIFAUNAS

The avifauna revealed in the fossils at hand is far from comprehensive, as it includes species from only three orders of birds, the Anseriformes, Galliformes, and Accipitriformes. Hawks, of moderate to large size, are most abundant (eight species) with two forms of gallinaceous birds and one goose, a total of eleven species in all. The lower Snake Creek beds, considered by Dr. Matthew to constitute an Upper Miocene horizon, contained more remains of birds than the Lower Pliocene levels. The Sheep Creek deposits have yielded two hawks. The following tabulation indicates the occurrence of species in the material studied, all of those listed, even where determination is not definite, belonging to forms that are now extinct.

##### LOWER PLIOCENE

*Ortalis phengites*, new species  
Galliformes (indeterminate)  
*Geranoaëtus conterminus*, new species

##### UPPER MIOCENE

Anserinæ (indeterminate)  
Buteonidæ (indeterminate)  
Buteonidæ<sup>3</sup> (indeterminate)  
*Aquila* species  
*Buteo typhoius*, new species  
*Geranoaëtus contortus*, new species

##### MIDDLE MIOCENE

*Urubitinga enecta*, new species

##### LOWER MIOCENE

*Proictinia effera*, new species

<sup>1</sup>1909, 'A Pliocene Fauna from Western Nebraska,' Bull. Amer. Mus. Nat. Hist., XXVI, pp. 361-365.

<sup>2</sup>1915, 'Additions to the Fauna of the Lower Pliocene Snake Creek Beds,' Proc. Amer. Phil. Soc., LIV, pp. 73-78.

<sup>3</sup>Level of occurrence, according to Dr. W. J. Sinclair, somewhat in question, possibly Lower Pliocene (see p. 507).



The hawks, which comprise the bulk of the species listed, are from groups whose modern representatives are frequently attracted by carrion, a habit that, if supposed to exist in these ancient forms, perhaps may account for the extensive representation of these birds in deposits that contain abundant remains of other vertebrates. Though no asphalt was present here as at Rancho La Brea, in California, Dr. Matthew suggests that mammals may have been entrapped by other means, possibly by quicksands.

The golden eagle listed, so far as may be told, is closely allied to the modern species. The *Buteo* described is a species of large size. The presence of two species of long-shanked eagles of the genus *Geranoaëtus* is of interest since the modern representative of the group, *G. melanoleucus*, is known now only in South America, where it ranges from the Straits of Magellan north through the pampas of Argentina to Uruguay and Paraguay, and, avoiding the tropics, extends northward through the Andes into Venezuela.<sup>1</sup> In geologic history *Geranoaëtus* first appears in the species here described from the lower beds of the Snake Creek which are supposed to be Upper Miocene. It is continued by an allied form in the higher, Lower Pliocene, deposits of the same formation, and is found in the asphalt beds of Rancho La Brea, in California, from which L. H. Miller<sup>2</sup> has described *G. grinnelli* and *G. fragilis*, both based on several specimens. The first seems to have been quite closely allied to *G. melanoleucus*, while the second, of more slender form, may prove to be a *Urubitinga*. A humerus and a coracoid secured among Pleistocene deposits from Hawver Cave, Eldorado County, California, are said by Miller<sup>3</sup> to be closely similar, if not indeed doubtfully distinct<sup>4</sup> from the modern *Geranoaëtus melanoleucus*. Thus we have long-shanked eagles of this assemblage appearing first in North America in the Snake Creek beds of Nebraska and continuing at least well into the Pleistocene in California. Their extermination in the north perhaps may be attributed to severity of the climate that in the Pleistocene replaced the mild temperatures of the preceding age. The fact that the modern *G. melanoleucus* in South America appears little affected by cold has no bearing on this statement as it indicates merely a species now fitted to live under temperate rather than subtropical conditions.

*Urubitinga enecta* introduces another group of long-legged buteonids that today ranges from Argentina north to southern Arizona and the

<sup>1</sup>It may be rare in its northern range as it is not mentioned in Chapman's, 1917, 'Distribution of Bird-Life in Colombia,' Bull. Amer. Mus. Nat. Hist., XXXVI.

<sup>2</sup>1911, Univ. California Publ. Geol., VI, pp. 314-315.

<sup>3</sup>1911, Univ. California Publ. Geol., VI, pp. 392-393.

<sup>4</sup>See Miller, L. H., 1912, Univ. California Publ. Geol., VII, p. 75.



lower Rio Grande Valley in Texas. *Morphnus daggetti* L. H. Miller<sup>1</sup> from the Pleistocene of Rancho La Brea is perhaps a near relative, as may be *Geranoaëtus fragilis* described by Miller from the same deposits. *Proictinia effera* is the first indication of the group of milvine hawks on this continent. It is remarkable that there is no representative of the Falconidæ among all of the species secured from these deposits.

The discovery of an extinct guan (*Ortalis*) in the typically Lower Pliocene levels of the Snake Creek beds is of considerable interest since the modern representatives of the group are Neotropical. In fact, the Penelopinae, the subfamily of the Cracidæ concerned, are confined largely to tropical and subtropical areas of South America, where they range southward to northern Argentina. A few are known in Central America and Mexico (*O. vetula* reaching to the lower Rio Grande Valley in Texas) while a *Pipile* is found on Trinidad and an *Ortalis* on Tobago, islands that, though they appear at the southern end of the Lesser Antillean chain, are South American rather than West Indian in their modern fauna. The presence of *Ortalis phengites* in northwestern Nebraska is indicative not only of the mild climate supposed to have prevailed during the Pliocene but, since this genus is arboreal, of heavy forest growth of fair extent at least along streams.

Several specimens in fragmentary condition in the collection have been referred simply to family. It is hoped that additional material from further exploration may yield bones from which these may be properly characterized.

Drawings to illustrate the new species described have been made by Miss L. Wieser.

#### Phasianidæ?

GALLIFORMES INDETERMINATE.—A right tibio-tarsus (Amer. Mus. Nat. Hist., Div. Pal. No. 1763), complete save for the head, from the Lower Pliocene level comes from a gallinaceous bird of uncertain affinity. In general form it is rather similar to *Canachites* but is much larger. Apparently it represents a bird with rather slender limb bones slightly taller than the modern sage grouse. The fossil is peculiar in having a very broad supra-tendinal bridge on the anterior lower end, a character in which it resembles the Cracidæ and differs from either the true pheasants, so far as they are represented in the collections of the National Museum, or the grouse of the New World. In other points, however, it seems near *Canachites*, *Dendragapus*, and *Centrocerus*. From the top

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<sup>1</sup>Condor, 1915, p. 179.



of the peroneal ridge to the distal end of the condyles this bone measures 104.0 mm. The greatest transverse breadth through the peroneal ridge is 8.2 mm., the least transverse breadth of the shaft 6.0 mm., and the greatest width across the condyles 12.0 mm.

At present the specimen may not be identified save to order.

### Cracidæ

#### *Ortalis phengites*,<sup>1</sup> new species

CHARACTERS.—Similar to *Ortalis vetula* (Wagler)<sup>2</sup> but slightly smaller; humerus (Figs. 1 and 2) with entepicondylar process relatively larger and longer; surface for attachment of pronator brevis muscle longer; shaft of bone somewhat more slender.

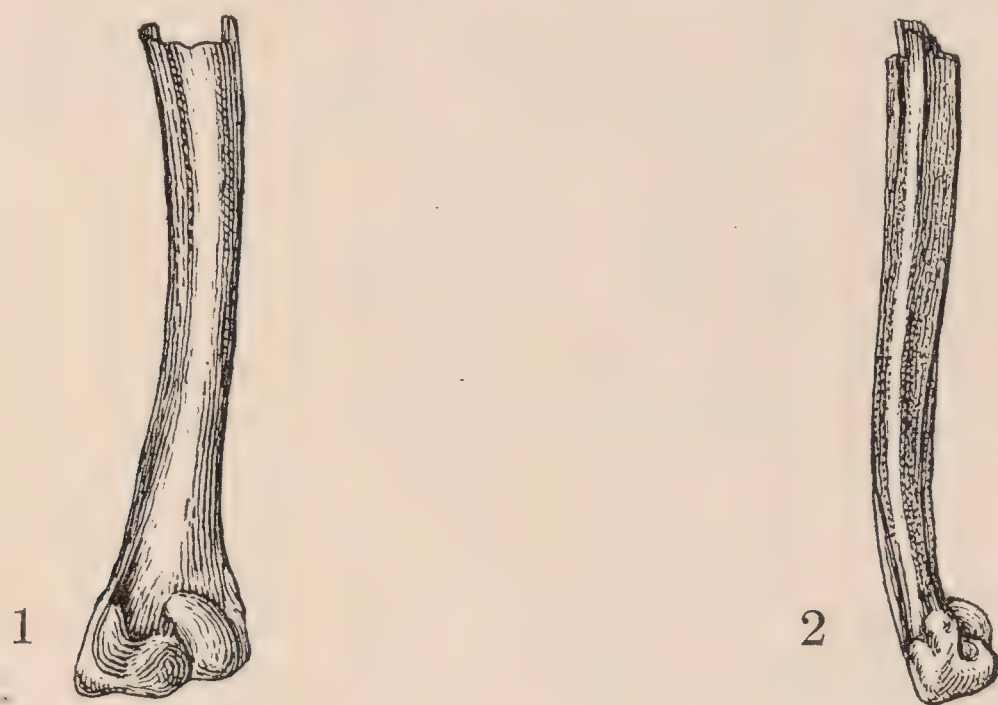


Fig. 1.—*Ortalis phengites*. Anterior view of left humerus (type), natural size.

Fig. 2.—*Ortalis phengites*. Internal view of left humerus (type), natural size.

DESCRIPTION.—Type, Cat. No. 426, collection of Harold J. Cook, left humerus with head missing, from the upper series of Snake Creek beds (Lower Pliocene) south of Agate, Sioux Co., Nebraska, collected by Harold Cook. Head of bone missing; shaft slender in middle expanding gradually toward either extremity, distinctly sigmoid, and flattened when viewed from front or back; curving toward front at lower end above support of trochlea, and slightly toward rear at upper end; nutrient foramen apparently closed; pit for attachment of brachialis anticus irregularly oval, small, but distinctly impressed; ectepicondylar process slight; shelf on anterior face external to base of radial trochlea narrow; radial trochlea moderately elongate and smoothly rounded, with upper base descending to meet shaft at a sharp angle, with a slight overhang on upper margin; inner margin slightly concave beyond level of ulnar trochlea, lower margin rounding smoothly into end of bone; ulnar trochlea globular on outer end, continued toward inner margin as a constricted ridge, projecting anteriorly to level of radial trochlea, rising at an oblique but marked angle above the shaft; attachment for pronator brevis elevated as a level plane above pit for brachialis

<sup>1</sup>A transparent mineral substance known as *phengites* (φενγίτης) was used at times by the ancients to close window openings. We may look on the bone here described as a window through whose meager transparency we may secure, indistinctly, a glimpse of the past.

<sup>2</sup>*Penelope vetula* Wagler, 1830, Oken's Isis, p. 1112. (Mexico.)



anticus, rudely triangular in form, about as long as broad; entepicondylar process twice as high as broad, narrow and elongate, olecranal depressions sharply impressed at inner side where the margin is abrupt, gradually disappearing toward center; sulcus anconeus medius broad, plane, not definitely impressed; sulcus anconeus lateralis narrower, plane, also not distinctly impressed; intertrochlear sulcus a shallow groove; ulnar trochlea continued distally considerably beyond level of radial trochlea; outer portion of ulnar trochlea not projected to any marked degree beyond level of inner (medial) portion.

MEASUREMENTS.—Greatest breadth across trochlea, 11.5 mm.; transverse diameter of shaft at center, 4.5 mm.

The type and only known specimen of the present species, according to the collector, Mr. H. J. Cook, was found associated in position with numerous mammalian fossils, among them the type specimen of the primate *Hesperopithecus haroldcooki* Osborn, in deposits that included *Hipparion* remains. It represents the first known record for a member of the family Cracidae in a fossil state.

The only other fossil peristeropodous galliform that seems to have been described to date (unless some member of that group is hidden among the many poorly described fossils that have been placed in the phasianine group) is *Gallinuloides wyomingensis* Eastman<sup>1</sup> from the Green River shales (Eocene) of Wyoming. Dr. Lucas<sup>2</sup> considers this as representative of a peculiar family, the Gallinuloididae, related to the Cracidae but differing from that group in the absence of a recurved posterior mandibular process, in the form of the short, stout, U-shaped furculum with its large hypocleidium, and in the shape of the articular facet for the coracoid. Dr. Shufeldt<sup>3</sup> in a later review has considered *G. wyomingensis* a true grouse related to *Lagopus* and *Bonasa*, evidently overlooking the fact that *wyomingensis* has the hallux on a level with the three anterior toes, and the inner notch on the posterior border of the sternum shallower than the outer one, both prominent characters that distinguish the peristeropodous from the alectoropodous section of the Galliformes.<sup>4</sup>

*Ortalis phengites* is distinctly smaller than *O. vetula*, a modern species that now extends from northern South America north barely within the confines of the United States in the lower Rio Grande Valley in Texas. It differs from the still larger *O. canicollis* of southern Brazil, Paraguay, and northern Argentina in more poorly developed ectepicondylar process, in relatively narrower, more elongate entepicondylar process

<sup>1</sup>1900, Geog. Mag., February, pp. 54–58.

<sup>2</sup>1900, Bull. Mus. Comp. Zool., XXXVI, pp. 79–84, 1 pl., 1 text fig.

<sup>3</sup>1915, Journ. Geol., XXIII, pp. 619–634, 2 figs.

<sup>4</sup>The fossil described as *Gallinuloides prentici* Loomis (1906, Amer. Journ. Sci., (4) XXII, pp. 481–482) is said by Shufeldt (1915, Trans. Connecticut Acad. Arts Sci., XIX, p. 42) to belong in the family Gruidae.



and relatively larger radial trochlea. In *O. vetula* (two specimens) the transverse diameter across the trochlea is 11.9 mm.; the diameter of the shaft at its center is 5.2 mm. The same measurements in *O. canicollis* are respectively 12.8 mm. and 6.3 mm. The slenderness of the shaft in *O. phengites* is especially to be noted. It may be observed that the humerus in the Meleagridæ and Phasianidæ (including the grouse and quails) has the globular portion of the ulnar trochlea projected beyond the level of the ridge that extends toward the entepicondylar process. This peculiarity is least noticeable in the turkeys and has its greatest development in the quails. The Cracidæ differ in that the trochlea in question has the two portions extended distally to practically the same level.

*Ortalis phengites* from the specimen seen is distinctly of the same type as our modern *chachalacas*, *charatas*, and *jacus*, tree-haunting forms of guans, with slender bodies and tails of long, broad feathers, that are noted for their harsh, raucous voices. Its presence in the Pliocene of Nebraska would seem to indicate heavy forests that at least must have bordered the streams. The Snake Creek beds mark the most northern record for its family, the Cracidæ, whose species in modern times are tropical and subtropical in occurrence.

### Anatidæ

ANSERINÆ INDETERMINATE.—A right ulna (Amer. Mus. Nat. Hist., Div. Pal. No. 1764) from the Upper Miocene levels belongs to a gooselike bird apparently somewhat related to the modern genus *Branta*, particularly to *Branta canadensis*. From this species the fossil, a bird about as large as *Branta c. minima*, differs in particular in conformation of the proximal end of the bone while at the opposite end it has a somewhat lower carpal ridge. As characters found in the ulna of birds usually are generalized it is not deemed expedient to describe the bird from this bone. It may be noted that the extinct form does not appear to be generically identical with modern species.

Though anserine birds have been known from Middle and Upper Miocene deposits in France or even from supposed Oligocene beds, they have not been recorded previously in North America from below the Pleistocene (though the writer has identified a fragment of a *Branta* from what are supposed to be Pliocene deposits in Arizona).

### Buteonidæ

#### *Buteo typhoius*, new species

CHARACTERS.—Metatarsus (Figs. 3 and 4) similar to that of *Buteo borealis* (Gmelin)<sup>1</sup> but considerably larger; lower end of metatarsus with a distinctly impressed anterior groove extending nearly to internal trochlea.

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<sup>1</sup>*Falco borealis* Gmelin, 1788, 'Syst. Nat.,' I, pt. 1, p. 266. (Carolina.)



DESCRIPTION.—Type, Cat. No. 1754, Dept. Vert. Pal., American Museum of Natural History, distal two-thirds of right metatarsus, from Upper Miocene level of the Snake Creek beds, 23 miles south of Agate, Sioux Co., Nebraska, collected by Whitford and Stoll in 1916.

External face of metatarsus flattened, slightly concave at center and rounded toward anterior and posterior margins, forming an approximately plane surface that slopes from its outer margin behind toward the median line to form a sharp anterior median ridge, broad and expanded at upper part, where the upper end has been broken away and lost, continuing thus for half its length, and then contracted

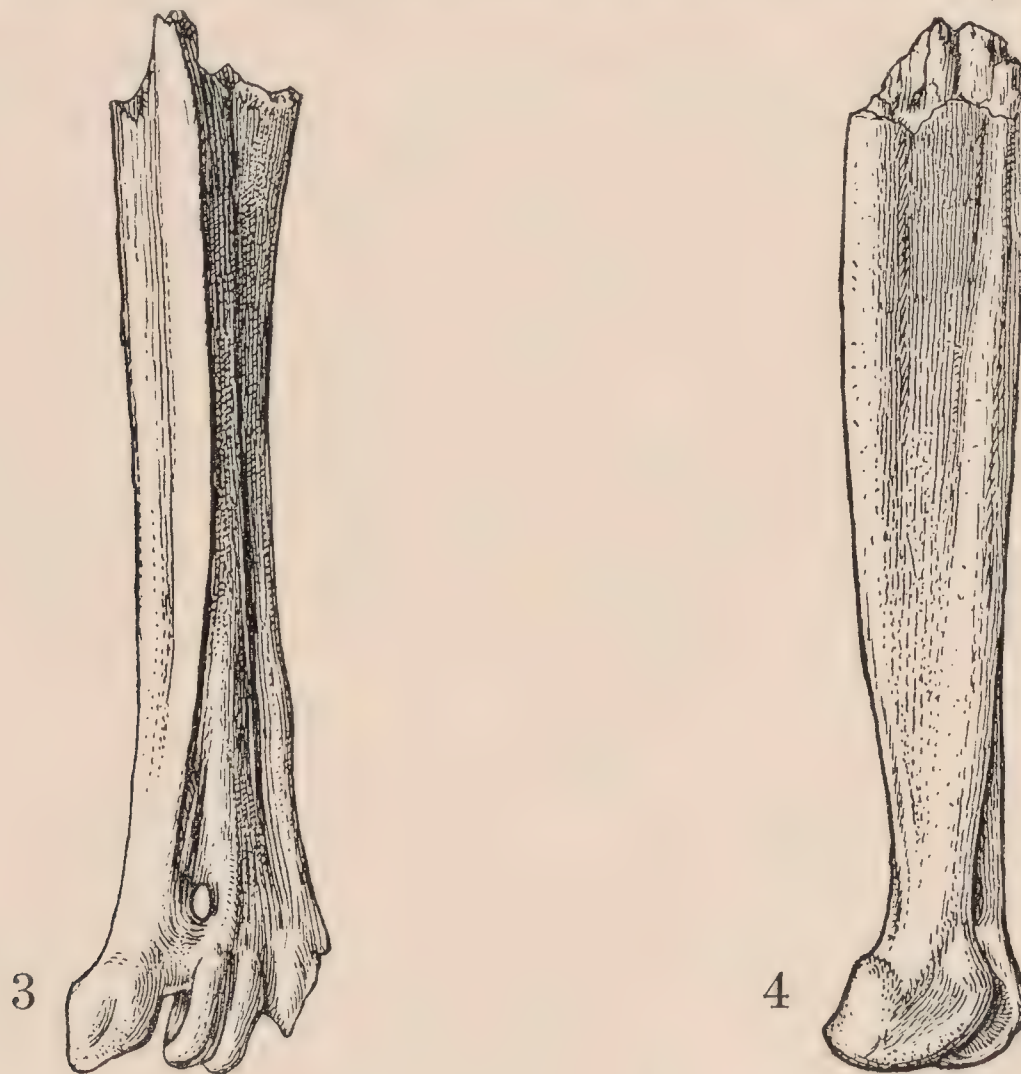


Fig. 3.—*Buteo typhoius*. Anterior view of lower part of right tarso-metatarsus (type), natural size.

Fig. 4.—*Buteo typhoius*. External face of right tarso-metatarsus (type), natural size.

gently to merge at the level of the distal foramen with a rounded surface that passes over to the base of the external trochlea; inner side of anterior face less regular in its contours; the anterior groove (proximal end missing) present as a shallow excavation in the sloping inner side of the anterior face; shaft constricted gradually with consequent restriction of the anterior groove, until the latter becomes a shallow impression of narrow width on the nearly plane surface of the inner face; the shaft, viewed from in front, appearing in horizontal profile near its center like an isosceles triangle; the shaft expanded once more below the center and flattened as the anterior ridge swings toward the outside; the anterior groove continued as a well-marked depression past the attachment of the hallux to disappear on the broadened space that supports the base of the outer trochlea; inferior foramen large, elongately elliptical, placed at the lower end of an impressed groove that begins on the inside of the central anterior ridge of the shaft, becomes better marked and deeper as the shaft



broadens distally, and then ends abruptly at the lower margin of the foramen; posterior surface broadly and regularly grooved to the level of the upper end of the attachment for the hallux where the bone expands, remaining very slightly concave; attachment for fourth metatarsal excavated as a shallow pit at upper end, below becoming less distinct, flattened and then slightly convexly rounded; viewed from in front the line of attachment is gently concave; the internal trochlea broken away; middle trochlea rather short, somewhat elongated posteriorly, distinctly inclined toward the outer one; its inner and outer faces concave, with a deep groove passing around it; posteriorly the raised outer margin prolonged to the base of the trochlea; the inner margin terminates below the attachment of the trochlea and is swung slightly inward; the groove is deeper on the posterior face than elsewhere; external trochlea narrow, the outer margin produced posteriorly as a thin flattened process that flares outward to a slight extent; outer face rounded gently, slightly excavated near center, inner face concave; the trochlea swung outward at a slight angle with the main axis of the bone; a canal leading upward through the bone from the center of the external intertrochlear sulcus to the lower, external margin of the inferior foramen; the middle trochlea projecting farther forward than the two lateral ones.

MEASUREMENTS (Of type).—Smallest transverse diameter of shaft, 9.2 mm.; transverse breadth at level of lower margin of inferior foramen, 14.0 mm.; greatest width of external face, 11.7 mm.; antero-postero diameter of external face of outer trochlea, 10.2 mm.

In addition to the broken metatarsus chosen as type *Buteo typhoius* is represented in the same collection by the distal third or more of a right ulna (No. 1757), and a nearly complete left coracoid (No. 1756). The fossil species is evidently similar to the modern red-tailed hawk (*Buteo borealis*) save that it is about one-half larger. The marked impression of the anterior groove on the shaft of the metatarsus as far as the digital facet for the first metatarsal is lacking in modern *Buteo* and is developed to an equal degree among related species only in *Heterospizias meridionalis* (Latham), a species of South American range with a long slender metatarsus of otherwise decidedly different proportions and appearance. Because of this marked anterior groove it is probable that, were *Buteo typhoius* a living bird, ornithologists would assign it to a distinct genus, but in its fragmentary condition it is deemed best to place it in the genus *Buteo*, which it resembles closely in other particulars.

The broken ulna secured has a conformation similar to that of *Buteo borealis* save that its tubercles and ridges are relatively less prominently developed. The bone is well fossilized but has the hollow of the shaft empty. The external face of the shaft is slightly flattened. The carpal ridge is broad, winglike, and produced below, but forms less of an angle with the line of the shaft and has the free proximal margin less angular than in *Buteo borealis*. The inferior radial depression begins slightly above the free upper margin of the carpal articulation and forms a broad elongated depression that terminates at the side of the carpal



tuberosity. It is marked by slight concavities at upper and lower end. The carpal tuberosity is strongly formed but any peculiarities that it possessed have been worn away so that it appears as a mere projection toward the inner side with the tip truncated and concave. The tendinal groove is deeply impressed. The bone exhibits the following measurements: diameter of shaft on external surface, 7.5 mm.; diameter on external surface through carpal ridge, 12.5 mm.; length of carpal ridge, 12.7 mm.



Fig. 5.—*Buteo typhoius*. Outer view of left coracoid, natural size.

The coracoid (Fig. 5) associated with the other remains is nearly entire, as it lacks only the attenuated processes of the hyosternal apophysis, the subclavicular apophysis of the precoracoid, and the extremity of the brachial tuberosity. The bone differs from that of *Buteo borealis* in certain particulars. The opening that gives passage to the supracoracoidal nerve is placed relatively somewhat nearer the scapular facet. The clavicular facet is much broader and more nearly plane, and the lower portion of the intermuscular line on the shaft lower, and less angular. In addition the shaft is relatively broader and heavier. The sternal facet shows a broad articular surface that extends well outward. The glenoid facet is slightly longer than wide and is somewhat elliptical, with the inner margin flattened. This bone measures as follows: length, from acrocoracoid to base at center, 49.3 mm.; smallest transverse diameter of shaft, 8.1 mm.; distance from top of acrocoracoid to upper margin of subclavicular foramen, 22.0 mm.

#### ***Geranoaëtus contortus*, new species**

CHARACTERS.—Metatarsus (Figs. 6 to 9) similar to that of *Geranoaëtus melanoleucus* (Vieillot)<sup>1</sup> but larger, and relatively more robust; tubercle for tibialis anticus placed higher on shaft; anterior surface more deeply excavated below head; internal superior foramen opening, on posterior surface, inside of sloping base of talon.

DESCRIPTION.—Type, Cat. No. 1758, Dept. Vert. Pal., American Museum of Natural History, left tarso-metatarsus, from Lower Snake Creek beds (Upper Miocene), collected in a deposit near Sinclair Draw, Sioux County, 20 miles south of Agate, Nebraska, in 1916 by Whitford and Stoll.

Proximal face of head rudely rectangular, the external glenoid facet slightly concave, the internal one larger, considerably excavated; intercondylar tubercle broad and slightly elevated, the internal glenoid facet at a lower level than the outer

<sup>1</sup>*Spizaëtus melanoleucus* Vieillot, 1819, Nouv. Dict. Hist. Nat., XXXII, p. 57. (Paraguay.)



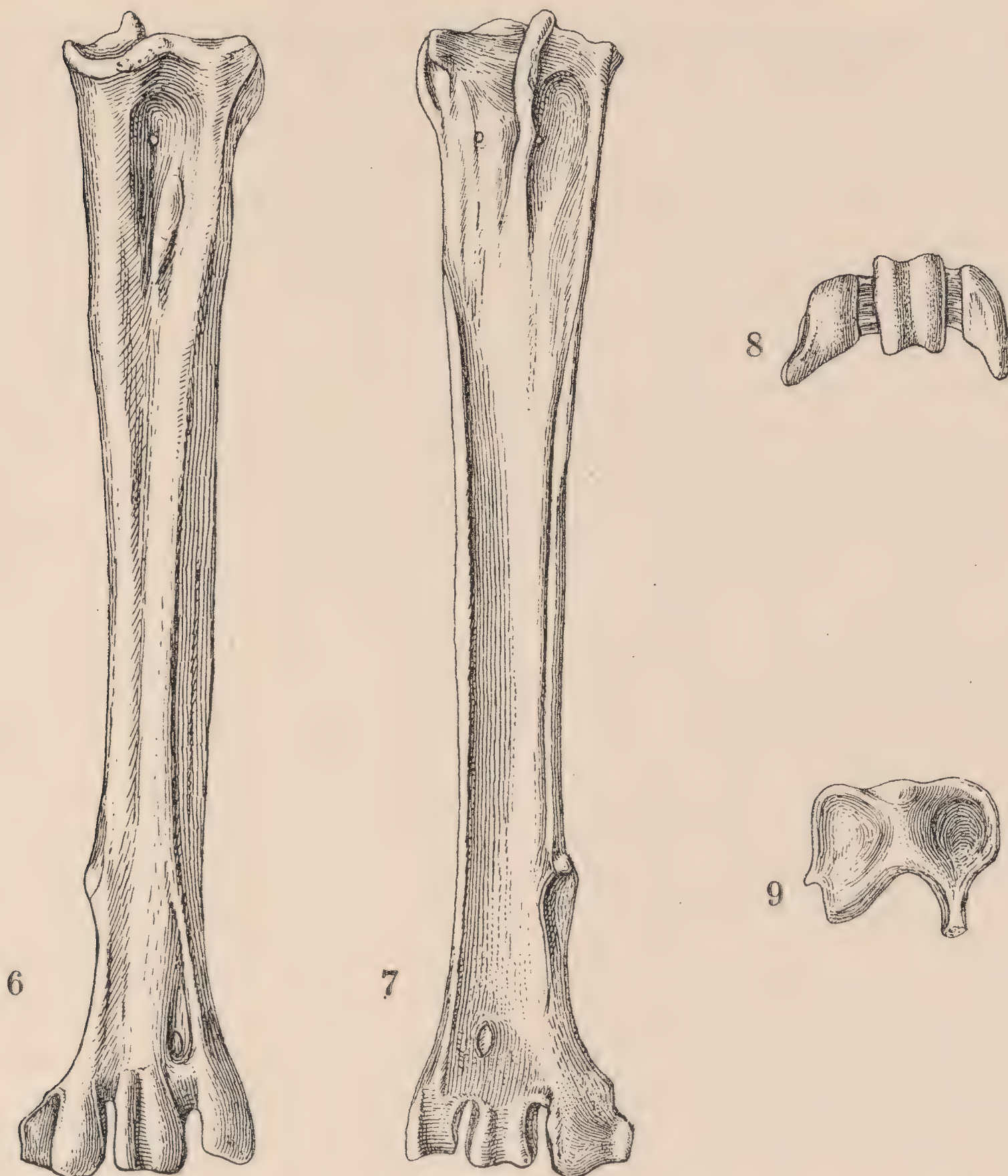


Fig. 6.—*Geranoaëtus contortus*. Outer view of left tarso-metatarsus (type), slightly more than natural size.

Fig. 7.—*Geranoaëtus contortus*. Inner view of left tarso-metatarsus (type), slightly more than natural size.

Fig. 8.—*Geranoaëtus contortus*. Distal outline of trochleæ of left tarso-metatarsus (type), natural size.

Fig. 9.—*Geranoaëtus contortus*. Proximal view of head of left tarso-metatarsus (type), natural size.

one; anterior semilunar groove nearly obsolete; posterior semilunar groove deep, the internal margin nearly at a right angle with the transverse plane of the shaft, the external margin sloping outward at a right angle to the same margin; external side of head square, the internal side rounded; a narrow, deeply excavated pit on the anterior face of shaft at upper end, the upper margin abrupt, with a sharp overhang of the head; the two superior foramina contained in this pit, below which the floor of the



depression slopes toward the front and then merges gradually with the anterior groove; external crest of transverse ligament (for tendon of extensor digitorum communis) very slightly indicated; internal crest of transverse ligament slightly stronger; space between only slightly flattened; tubercle for tibialis anticus strong, located slightly external to center of shaft; shaft moderately strong, only slightly expanded at upper end, contracting gradually to center, then continued to expand to support the trochlea, triangular in cross section in general, becoming flattened below, marked on anterior side by anterior sulcus which becomes shallow a short distance below tubercle of tibialis anticus and continues as a slightly impressed, rather narrow channel along inner side of median line to disappear at the level of the attachment for the first metatarsal; outer face of shaft almost plane, with a very gradual curve inward toward middle; external ligamentous ridge rather slight; below this point the anterior margin of shaft straight, meeting the anterior surface at a sharp angle; posterior margin of external face curving to form an expanded flat surface that gradually increases to middle and then contracts again at the level of the inferior foramen; inferior foramen moderately large, located at the bottom of a groove that begins shallowly and becomes much depressed as it continues downward; surface of shaft internal to this groove nearly flat; inner margin of shaft compressed to a thin plate that is straight at first, and then swings in a gradual posterior curve, that below the middle again returns toward the front until it is interrupted by the projecting crest that marks the proximal margin of the attachment of the first metatarsal, below which the line of the shafts wings outward to support the base of the outer trochlea; external head of talon somewhat rounded, knoblike, proximally slightly raised above level of external glenoid facet, with abrupt external margin cut by a slight notch, and internal and posterior margins sloping gradually into body of shaft; internal head of talon thin, bladelike, projecting, with free margin cut by two slight concave irregularities on inner side, posteriorly inclined slightly inward as an overhang; proximal margin raised above proximal articular surfaces, posteriorly, after forming a square, projecting blade, descending in an abrupt slope to level of shaft along which it continues as a raised line for a space of fifteen millimeters; internal superior foramen lying inside of elongated base line of external head of talon; external superior foramen, at same level, located below base of external head of talon; posterior face of shaft excavated to form a broad groove bounded laterally by crests formed by the posteriorly raised margins of the external and anterior surfaces, the groove terminating at the level of the upper end of the articulation of the first metatarsal; the shaft below this point plane to the level of the inferior foramen where there is a shallow excavation that extends across the center of the bone; articular facet for first metatarsal cut at an oblique angle into the inner side, the raised line of the internal margin of the anterior surface of the shaft terminating above the commencement of the articulation; the facet deeply excavated at first, bounded above by a raised ridge, and merging below into outline of side of shaft; external trochlea a flattened plate, swung slightly outward, compressed on posterior portion to a posterior projection one-half the width of the body of the trochlea; middle trochlea, somewhat broader, expanded slightly on external side, with lateral margins swollen and lateral faces concave, traversed by a strongly impressed groove that extends around entire articular surface, the external margin elevated slightly above the internal one, and the whole trochlea swung slightly toward the outside; internal trochlea with a broad, rounded base with a projecting, triangular winglike projection from the external posterior angle; a large, rather deep, excavation on the outer surface.



MEASUREMENTS (Of type).—Total length, 113.0 mm.; greatest breadth of head, 19.0 mm.; greatest breadth across trochlea, 23.0 mm.; smallest transverse diameter of shaft, 10.0 mm.; distance from center of tibialis anticus tubercle to upper end of shaft, 21.0 mm.

In the diagnosis of this species direct comparison has been made with *Geranoaëtus melanoleucus*, the only living member of the genus, confined at present to South America, where it ranges from Argentina and Brazil northward through the Andes into Venezuela. From *Geranoaëtus grinnelli* L. H. Miller<sup>1</sup> the species from Nebraska differs in slightly larger size, in greater elevation of the tibialis anticus tubercle, in reduced external crest of talon, and broader, more open, posterior semilunar groove. It is distinguished from *G. fragilis* L. H. Miller<sup>2</sup> by the same characters, and in addition has the shaft distinctly more robust. A third eagle of the long-shanked type, *Morphnus woodwardi* L. H. Miller,<sup>3</sup> is distinguished from *contortus* by larger size, less excavation below the head on the anterior face of the shaft, and greater breadth of the transverse supratendinal bridge. In comparing the Nebraska fossil with these three species I have been dependent for details on Dr. Miller's figures and descriptions.

*Aquila danana* Marsh<sup>4</sup> based on the condyles of a tibio-tarsus of doubtful Pliocene deposit seems to represent a hawk of questionable buteonid affinity. Marsh's type has been figured by Shufeldt.<sup>5</sup> From this illustration, and from the original description, it appears that the bird described as *A. danana* was smaller than *Geranoaëtus melanoleucus*, as the measurement across the condyles, said by Marsh to be "8 lines," is equivalent to a little more than 16 millimeters. *G. contortus* is considerably larger, sufficiently so to determine that it is not identical with *A. danana* as the difference in size is beyond the range of individual variation.

The material upon which *Geranoaëtus contortus* is based has been more comprehensive than usual with avian fossils of like age. With the type tarso-metatarsus are associated a right metacarpus (A. M. N. H. No. 1759) that lacks the distal end and most of the third metacarpal, and the outer end of a left ulna (A. M. N. H. No. 1760), both collected in the season of 1916, and possibly from the same individual that furnished the type. Further material secured in 1921 includes a right metatarsus (A. M. N. H. No. 1762), entire save for the outer trochlea and the intercondylar tubercle on the head, a fragmentary metacarpus (A. M. N. H.

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<sup>1</sup>1911, Univ. Calif. Publ. Geol., VI, p. 314. (Pleistocene, Rancho La Brea.)

<sup>2</sup>*Loc. cit.*, p. 315. (Pleistocene, Rancho La Brea.)

<sup>3</sup>*Loc. cit.*, p. 312. (Pleistocene, Rancho La Brea.)

<sup>4</sup>*Aquila dananus* Marsh, 1871, Amer. Journ. Sci. Arts, (3) II, p. 125. (Pliocene (?) Loup Fork.)

<sup>5</sup>1915, Trans. Conn. Acad. Arts Sci., XIX, Pl. II, figs. 13.



No. 1766), comprising the distal part of the second metacarpal with the outer end of the third, and a left radius (A. M. N. H. No. 1765), that lacks the proximal end. The two last mentioned were secured from the same quarry.

In the collection of Mr. H. J. Cook is found the proximal fourth of another right metacarpal (No. 465), broken squarely across a short distance beyond the proximal union of second and third metacarpals. This specimen was secured by Mr. Cook in April, 1922 at the same locality that yielded the material from the American Museum listed as collected in 1921 (A. M. N. H. Nos. 1762, 1765 and 1766). It is marked as taken in the lowest phase of the Snake Creek beds in what have been called the "Sheep Creek" deposits. (Allocation under the present species somewhat tentative.)



Fig. 10.—*Geranoaëtus contortus*. Inner face of broken left metacarpus, natural size.

The metacarpus (Fig. 10) of *G. contortus* as represented by three broken specimens, save for its larger size, is not notably different from that of *G. melanoleucus*. The articular facet for the pollex, on the first metacarpal, is relatively larger and has the surface more convexly rounded. The external groove (for the tendon of the extensor digitorum communis) in the fossil lies on the outer side of the second metacarpal, proximally approaching the upper margin, but not running along the upper surface as in *G. melanoleucus*. The pisiform process is strong and somewhat conical. Other differences from the modern bird are not noted. The greatest height of the head of the bone in the largest specimen is 23.3 mm.; the greatest transverse diameter of the second metacarpal, 8.8 mm.; of the third metacarpal, 7.8 mm.; the complete metacarpus was apparently about 100 mm. long. The metacarpus from the collection of Mr. Cook (No. 465) is smaller but is within the range of sexual variation in size in this group. It has a somewhat more porous texture on the ends of the projecting processes and may have come from an immature bird. The greatest height of the head in this specimen is 21.0 mm.; the greatest transverse diameter of the second metacarpal, 7.3



mm.; and of the third metacarpal, 7.5 mm. The bone is dark in color like the others.

The ulna, represented by a broken fragment (A. M. N. H. No. 1760), is closely similar to that of *G. melanoleucus* save that it is larger. The form in the fossil is so close to that in the modern bird that the slight differences perceptible are apparently such as occur in different individuals of the same species. The broken radius (A. M. N. H. No. 1765) assigned to this species is likewise almost identical with that of the modern bird save that it is of greater size. The angles of the lower end are slightly more rounded and the end of the bone is transversely more expanded. Otherwise the two are the same. The transverse diameter of the lower end in the fossil radius is 11.5 mm.; the transverse diameter of the shaft equals 4.7 mm.

The right tarso-metatarsus (A. M. N. H. No. 1762) collected in 1921 is somewhat distorted but is readily seen to be similar in form to the type. The bone is larger than the type as it has the following measurements: total length, 120.0 mm.; greatest breadth of head, 20.5 mm.; smallest transverse diameter of shaft, 10 mm.; distance from center of tibialis anticus tubercle to upper end of shaft, 23.0 mm. The general agreement in form in this bone to the type specimen is close. The tubercle for the tibialis anticus is slightly more prominent and is located nearer the outer margin. The internal head of the talon seems to have had a shorter base, but this is not certain as part of this crest has been broken away. Otherwise the two are closely similar save for the more massive proportions of the second fossil, a difference in size equal to that found as a sexual variation in an extended series of the modern *Buteo borealis*, a member of a genus allied to *Geranoaëtus*. There is nothing apparent to indicate that the two fossil bones may not be conspecific.

It appears that *Geranoaëtus contortus* was a long-shanked eagle of strong wing power, that may not have differed in any pronounced manner from the living *G. melanoleucus* save that it was of considerably greater bulk.

#### ***Geranoaëtus conterminus*, new species**

CHARACTERS.—Metatarsus (Figs. 11 to 13) similar to that of *Geranoaëtus contortus* Wetmore, but with inner trochlea broader and more massive, especially at base.

DESCRIPTION.—Type, distal half of left tarso-metatarsus, Cat. No. 12156, Princeton University Geological Museum, collected from the upper level of the Snake Creek beds (Lower Pliocene) at locality 1000 A (T. 26 N., R. 55 W., Sec. 31, N. E.  $\frac{1}{4}$ ) twenty miles south of Agate, Sioux County, Nebraska, in 1914, by Dr. W. J. Sinclair, A. C. Whitford and C. Barner.



External trochlea a flattened plate (with the posterior projection mainly broken away), swung slightly outward; articular portion narrow, laterally compressed, abrupt on inner margin, cut away on outer anterior angle, and faintly grooved on distal posterior part; excavated as a conical pit on outer face; sulcus between median and outer trochlea moderately deep, with an enclosed canal leading from the center of the sulcus to the lower margin of the inferior foramen; middle trochlea rather small, the free end swung slightly toward the external side, so that the projection appears to be set on the shaft at a slight angle; internal and external faces deeply excavated; trochlea strongly grooved; outer side of groove projecting slightly farther than

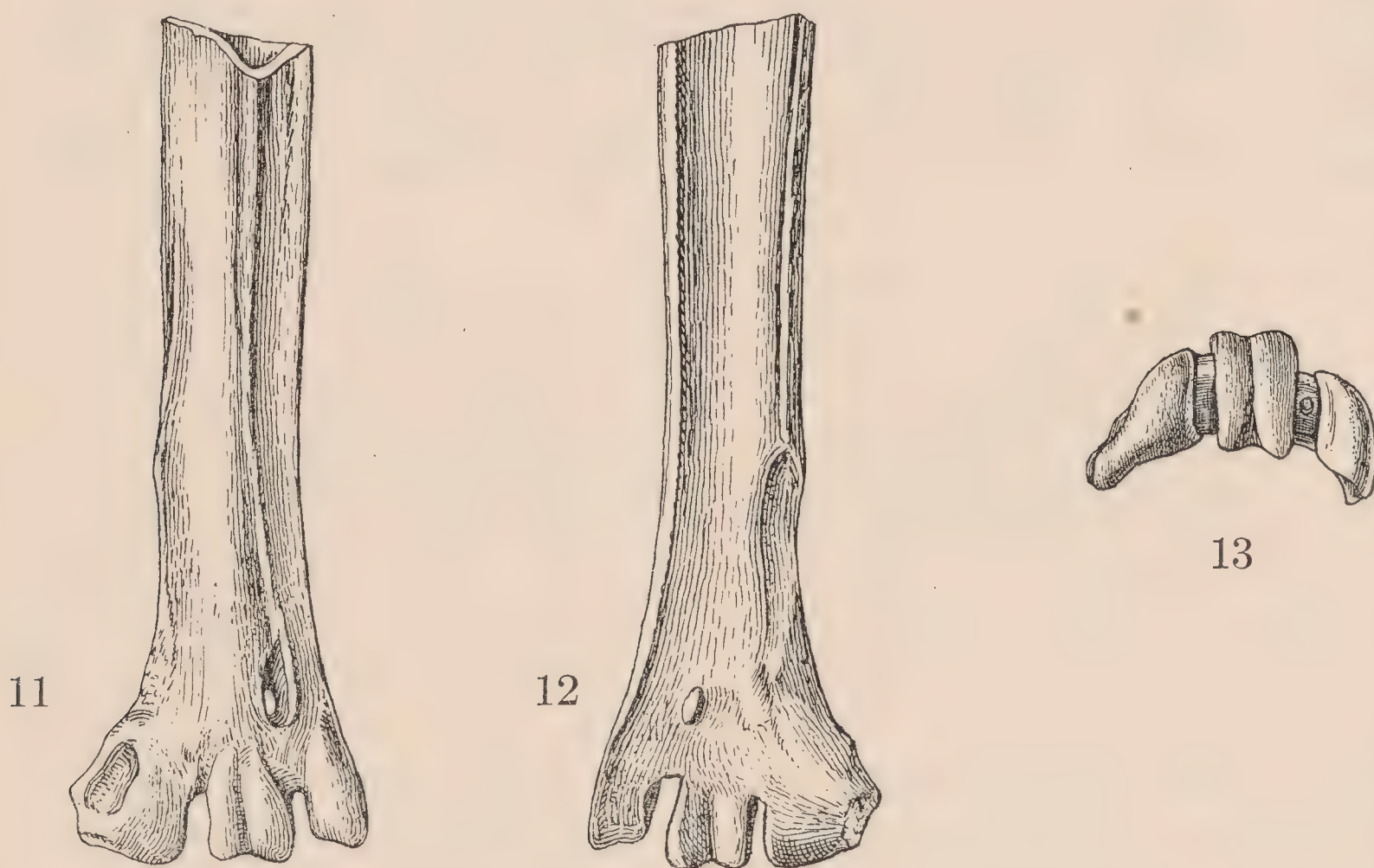


Fig. 11.—*Geranoaëtus conterminus*. Anterior face of broken left tarso-metatarsus (type), natural size.

Fig. 12.—*Geranoaëtus conterminus*. Posterior view of broken left tarso-metatarsus (type), natural size.

Fig. 13.—*Geranoaëtus conterminus*. Distal outline of trochleæ of left tarso-metatarsus (type), natural size.

inner, especially on posterior face; proximal end of outer face inclined rather abruptly inward and continued upward on shaft for a shorter distance than inner face; inner face straight save for a slight indentation at lower anterior margin; the whole trochlea swollen on anterior side to form a prominent projection beyond the level of the lower end of the shaft and of the two lateral trochlea; the raised margins of the central groove merging posteriorly with shaft at line of intertrochlear sulci, the inner one cut off somewhat abruptly at an oblique angle; inner trochlea broad and strong, projecting distally slightly beyond level of middle trochlea; inner intertrochlear sulcus slightly shallower and narrower than outer one; trochlea projecting at a right angle with the transverse plane of shaft, extending outward beyond line of shaft; base



broadened externally; inner portion rounded, with inner face deeply excavated; winglike projection broad, flattened, in outline a truncated cone with a deep concavity excavated on outer face; lower posterior margin gently curved; posterior surface flattened, but with surface somewhat faintly and irregularly concave; facet for first metatarsal broad and prominently excavated for upper half, below narrowed and merged with compressed margin of shaft, bordered anteriorly by a faint rounded line; inferior foramen moderately large, oval in form, with a short, shallow, broad groove continuous with its upper margin; shaft triangular, strong; outer face plane on posterior portion, rounded on upper portion, meeting the anterior face at a sharp angle throughout; anterior surface somewhat irregularly rounded on lower portion, where it is perforated on the outer side by the inferior foramen, and grooved by the shallow canal leading into this foramen, while in addition a *linea aspera* extends in an irregular curve from the internal sulcus back to the groove; this surface posteriorly rotated outward and more flattened; a broad, shallow, poorly indicated furrow extended down past the articular facet for the first metatarsal; posterior surface of shaft with margins raised to delimit a deep, broad groove on upper portion, flattened and nearly plane at level of first metatarsal attachment, and shallowly concave below in region of inferior foramen; middle of shaft triangular in cross-section.

MEASUREMENTS (Of type).—Greatest breadth across trochlea, 22.5 mm.; smallest transverse diameter of shaft, 11.0 mm. (Other useful measurements not available because of broken condition of specimen.)

The present species appears similar to *Geranoaëtus contortus* of the Upper Miocene beds in the same vicinity but is distinguished by the broadening of the basal support of the external condyle. Like the species just mentioned, *G. conterminus* may not be confused with the species known as *Aquila danana* Marsh because of its larger size. It was apparently similar to *G. contortus* but perhaps of slightly more robust proportions.

With the description of the present form we find that the group of long-legged eagles, represented by our living *Geranoaëtus melanoleucus*, is present in the Upper Miocene as *Geranoaëtus contortus* Wetmore, in the Lower Pliocene as *G. conterminus* Wetmore, and in the Pleistocene (Rancho La Brea) as *G. grinnelli* Miller and *G. fragilis* Miller. This type of raptorial bird, to judge from the available material, was well developed during the later Miocene and, on the evidence offered by the metatarsal bone, seems to have continued to the present day with only slight modification of form, but with a reduction in size and strength, as the fossil species that have been mentioned are all larger than the living bird.



**Urubitinga<sup>1</sup> enecta**, new species

CHARACTERS.—Tibio-tarsus (Figs. 14 to 16) similar to that of *Urubitinga u. ridgwayi* Gurney<sup>2</sup> but considerably larger; anterior groove on lower face of shaft (above tendinal bridge) more extensive; space between this groove and outer face of bone narrower; lower margin of external condyle farther produced.

DESCRIPTION.—Type, Cat. No. 6300, Dept. Vert. Pal., American Museum of Natural History, left tibio-tarsus (somewhat crushed), from the lower Sheep Creek beds (early Middle Miocene) collected in quarry 20 miles south of Agate, Sioux County, Nebraska, in 1922, by A. Thomson. Shaft of bone flattened and slightly distorted, restored by the skill and meticulous care of Mr. Thomson nearly to original condition.

Outer face of external condyle rounded in outline, projecting farther in front than in rear, excavated centrally to form an oblong pit, bounded, save above, by the heavy rounded margin of the condyle, this margin being narrower on posterior side than below or in front; a low, elongate tubercle on lower side of shaft immediately above the depression mentioned; anterior face of external tubercle flattened, sloping inward to join at a sharp angle the perpendicular wall of the intercondylar fossa that bounds the inner side; lower face somewhat rounded, sloping gradually into intercondylar sulcus, merging gradually into the plane of the posterior surface with gentle inward slope; internal condyle not as high as external one, projecting anteriorly for nearly half of antero-posterior diameter, a considerably greater distance than in case of the external condyle, a circumstance due to the narrower form of the inner side of the shaft; outer face of inner condyle deeply excavated, with a large, rounded tubercle projecting at its center; this excavation bounded by a strongly raised ridge, save above, posterior to median tubercle where the depression passes as an open trough to side of lower posterior face of shaft; internal condyle projecting outward beyond line of shaft more than outer condyle; intercondylar sulcus broad, shallow with gently rounded bottom, the median point located slightly nearer the outer condyle; intercondylar fossa deeply incised to level of base of shaft, bounded on outer side by nearly perpendicular wall, on the inner margin by a slightly less abrupt line; broad, nearly plane at bottom, with slightly deeper excavation on outer side, divided into two depressions by a low transverse median ridge, tendinal bridge (for extensor digitorum communis tendon) strong, somewhat arched, a broad area separating the groove that passes beneath it from the external margin of the shaft; groove for the peroneus profundus short but distinctly marked; shaft somewhat crushed and distorted (skillfully repaired), but sufficiently perfect to indicate its slender, flattened form, with compressed outer and broader inner margins; peroneal ridge long, strong, bladelike, elevated distally, where it passes to the body of the shaft by an abrupt declivity, merging more gradually into shaft above, excavated along base on posterior side;

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<sup>1</sup>In the present paper the generic name *Urubitinga* is used as in the 'A. O. U. Check-List,' 3rd Ed., 1910, p. 160. According to Opinion 62 of the International Commission on Zoölogical Nomenclature (Smiths. Inst., Publ. 2256, March 1914, pp. 147-149) it would appear that *Urubitinga* Lesson should be replaced by *Morphnus*, since Gray in 1841 established *Falco urubitinga* Gmelin as the type of *Morphnus* Cuvier, 1817 (actual date December 7, 1816). Mathews (1915, Austr. Av. Rec., III, p. 10) has brought to attention the fact that *Morphnus* was first published (as of Cuvier) by Dumont in the continuation of the 'Dictionnaire des Sciences naturelles par plusieurs Professeurs du Jardin du Roi, etc.,' I, Suppl., October 12, 1816, p. 88. It seems doubtful that Gray's action with regard to type fixation of *Morphnus* Cuvier will hold for *Morphnus* Dumont of earlier date, so that *Urubitinga* may for the present be considered valid.

<sup>2</sup>1884, 'List Diurn. Birds of Prey,' p. 77. (Mexico and Guatemala.)



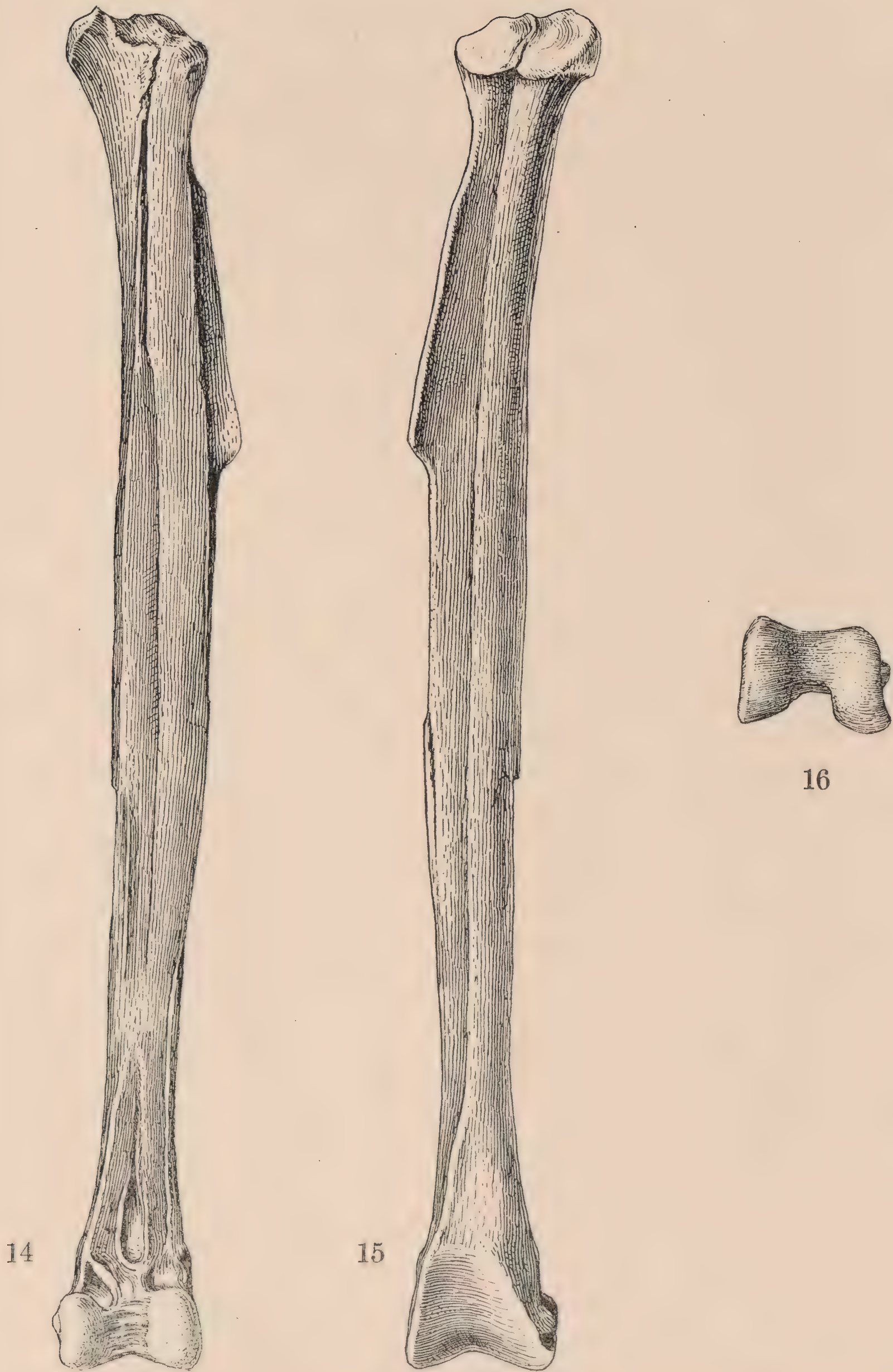


Fig. 14.—*Urubitinga enecta*. Anterior face of left tibio-tarsus (type), natural size.  
 Fig. 15.—*Urubitinga enecta*. Posterior surface of left tibio-tarsus (type), natural size.  
 Fig. 16.—*Urubitinga enecta*. Distal outline of condyles of tibio-tarsus (type), natural size.



posterior margin of head deeply notched in middle; a high central tubercle; remainder of head considerably damaged.

MEASUREMENTS.—Total length, 163.0 mm. (approximate); transverse breadth across condyles, 17.0 mm.; depth of internal condyle, 12.5 mm.; depth of external condyle, 12.5 mm.; length of articular portion of peroneal ridge, 32.0 mm.

In slender form and in the notching of the posterior margin of the head, characters found in the fossil here described, the tibio-tarsus in modern *Urubitinga* differs distinctly from other buteonids examined. In *Urubitinga* the transverse breadth of the lower condyles is equal to only about one-tenth of the total length, while in such species as *Geranoaëtus melanoleucus*, *G. contortus*, *Buteo borealis*, *B. galapagensis*, *Rupornis ridgwayi*, and *Heterospizias meridionalis* the lower end of this bone is distinctly broader. Though smaller buteos (notably *B. lineatus*) may be proportioned like *Urubitinga*, the larger forms have the tibio-tarsus distinctly stronger. The bone in *Heterospizias* is more slender than in other large hawks of similar size, but still is heavier than in *Urubitinga*.

Associated in a small pocket with type of *U. enecta* was found a left humerus that, through careful restoration, is nearly perfect, parts of two radii, and a nearly complete right scapula, that perhaps came from one bird; part of another radius represents some other hawk.

The peculiarities of the humerus are shown in the accompanying drawings (Figs. 17 and 18). It must be remarked that the humerus in the larger buteonids is remarkably similar in general appearance in species otherwise very distinct. The humerus now under discussion, which is strong and heavy, has the depression for the brachialis anticus restricted, with a broad, comparatively smooth, space separating that depression from the base of the ectepicondylar process, as in *Urubitinga ridgwayi*, and not as in *Geranoaëtus* and *Buteo*. The size of the humerus is a certain indication of the bulk and weight of this ancient hawk, which was apparently as large a bird as the two species of *Geranoaëtus* of Miocene times, but one with longer, more slender legs. Careful comparison of the fossil specimens shows that the tarso-metatarsus that articulated with the tibio-tarsus of *Urubitinga enecta* was even more slender than that of the modern *Geranoaëtus melanoleucus*, and consequently much lighter in form than that of *G. contortus* or *G. conterminus*.

Though *Urubitinga* is here first reported as a prehistoric genus, it is not improbable that some of the fossil hawks previously described may transfer to this group on careful comparison. Thus, the slender form and high location of the tubercle for the tibialis anticus seen in the metatarsus of the bird known as *Geranoaëtus fragilis* L. H. Miller indicate an approach toward *Urubitinga* and may perhaps be sufficient to transfer





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Fig. 17.—*Urubitinga enecta*. Posterior face of left humerus, natural size.  
Fig. 18.—*Urubitinga enecta*. Anterior face of left humerus, natural size.



the species to that genus. The degree of relationship of *Aquila danana* Marsh to *U. enecta* is somewhat uncertain. The type of *A. danana*, the broken end of a left tibio-tarsus,<sup>1</sup> apparently has the dimensions found in *U. enecta*, but differs in the outline of the lower margin of the condyles, and in other details.

#### **Aquila species**

The distal end of a left radius secured by the Princeton University Expedition of 1914 (at locality 1000 C in T. 25 N., R. 55 W., S. E. ¼ to middle of Sec. 3) is rather closely similar in form to that of a golden eagle (*Aquila chrysaetos*). The bone in question is slightly smaller than the radius of the modern golden eagle, and, save that the protuberances are more swollen, is similar in general outline. It is probable that it represents a larger species than the fossil *Aquila danana* Marsh. The fragment measures 12.5 mm. in transverse diameter across the head. It was taken from the Upper Miocene levels of the Snake Creek beds.

#### **Proictinia effera, new species**

CHARACTERS.—Larger than *Proictinia gilmorei* Shufeldt.<sup>2</sup> Metatarsus (Figs. 19 and 20) somewhat similar to that of *Ictinia mississippiensis* (Wilson)<sup>3</sup> but external crest of talon relatively lower, external ligamentous ridge more prominent, tubercle for tibialis anticus relatively higher on shaft; outer proximal margin produced posteriorly as distinct sharp-edged plate separated by a shallow groove from the external crest of the talon; much longer and slightly heavier.

DESCRIPTION.—Type, Cat. No. 6299, Dept. Vert. Pal., American Museum of Natural History, right tarso-metatarsus with inner side imperfect, from the Lower Harrison beds (Lower Miocene) collected in Agate Fossil quarry, Sioux County, Nebraska, by A. Thomson. Outer trochlea narrow, comparatively small and weak, with a slight platelike, posterior projection, and a slight depression on the outer and inner faces, separated by a narrow cleft from the middle trochlea; middle trochlea stronger, heavier, impressed with a shallow groove extending clear around, less perfect on inner side; inner and outer faces concave; inner trochlea broad with substantial base, separated by a narrow, straight-walled cleft from middle trochlea; outer wing broken away; inner trochlea produced distally slightly farther than middle one, middle trochlea extending slightly beyond level of outer one, the middle trochlea projected farther toward the front than the others; inferior foramen large, placed at the lower end of a long shallow groove; posterior face of lower end of shaft decidedly flattened, comparatively smooth; (articular surface for first toe missing); external face of shaft flattened, plane, bounded by sharply angular margins, widening in a gradual swell to near median line and then, as gradually, contracting toward head of

<sup>1</sup>Figured by Shufeldt, 1915, Trans. Conn. Acad. Arts Sci., XIX, Pl. II, fig. 13.

<sup>2</sup>*Proictinia gilmorei* Shufeldt, R. W., 1913, Bull. Amer. Mus. Nat. Hist., XXXII, p. 301, Pl. LV, fig. 27. Type, imperfect right coracoid (U. S. Nat. Mus. Cat. No. 6852) from Loup Fork Formation, "Lower Pliocene," Long Island, Phillips Co., Kansas, collected by J. B. Hatcher in 1884.

<sup>3</sup>*Falco mississippiensis* Wilson, 1811 Amer. Orn., III, p. 80, Pl. xxv, fig. 1. (A few miles below Natchez, Mississippi.)



bone to the narrow line of the external ligamentous ridge, broadly cut away at upper end, behind the ligamentary ridge mentioned, in a smooth slope that passes to the posterior surface of the bone; the external surface broadened again beyond the ligamentary ridge, continuing thus to end abruptly at the upper margin of the bone; lower end of front of shaft flattened, the greater part of the remainder of this surface missing; tubercle for tibialis anticus attachment large, located far up toward head of bone; a cuplike depression with distinctly outlined upper and lateral margins on anterior face below head; internal tubercle developed but cut away below where it descends toward shaft; outer proximal margin immediately below head produced as a sharp-edged plate separated from the small but elevated external crest of the talon by a shallow groove, this crest thus entirely on posterior face of bone; external

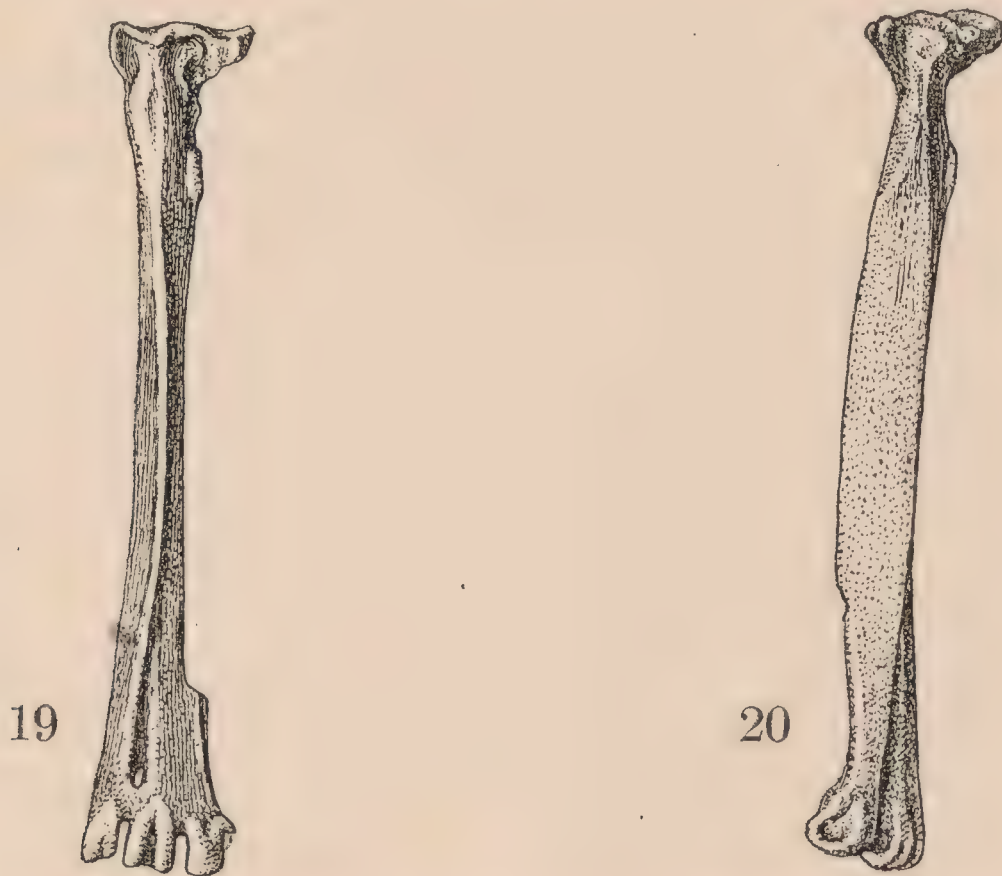


Fig. 19.—*Proictinia effera*. Anterior face of right tarso-metatarsus (type), natural size.

Fig. 20.—*Proictinia effera*. Outer surface of right tarso-metatarsus (type), natural size.

crest of talon perforated at tip by a small foramen; a broad shallow groove inward of this ridge; internal crest of talon broken away; glenoid facets on head shallow, the inner one deeper, with a raised outer margin; internal tubercle low and rounded; anterior semilunar groove faintly indicated; posterior semilunar groove distinct with rounded outline, rather narrow.

MEASUREMENTS.—Total length, 56.8 mm.; transverse breadth of head, 9.4 mm.; transverse breadth across trochlea, 9.4 mm.; distance from center of tubercle for tibialis anticus to upper end of bone, 9.6 mm.; width of external face at widest part, 5.3 mm.

The bird here under consideration needs comparison among other known fossil hawks only with *Proictinia gilmorei*, a genus and species named by Dr. Shufeldt from a broken coracoid, said to be from "Lower Pliocene, Loup Fork Formation, near Long Island, Phillips County, Kansas."



The type in question is apparently from a juvenile bird as it shows the porous, imperfectly ossified structure and lack of development of processes found in birds that have not yet attained adult stature. Immaturity is indicated too by the large size of the opening that leads from the inner side of the neural foramen to the cavity of the shaft. On careful comparison I find that the type of *Proictinia gilmorei* more nearly resembles the coracoid of the everglade kite, *Rostrhamus sociabilis* (Vieillot) than any other modern species, but is slightly shorter and a trifle more robust. It differs from *Rostrhamus* in the more central position of the tubercle on the dorsal face of the shaft, and in a slight thickening of the inner edge of the bone opposite this tubercle.

The metatarsus here described as *P. effera*, when compared with the metatarsus of *Rostrhamus*, is found to be decidedly longer and slightly heavier. By analogies derived from study of other kites I should expect *P. effera* to have a longer heavier coracoid than *Rostrhamus* or in other words it is my belief that *effera* represents a larger species than *P. gilmorei*. As *gilmorei* is known only from a coracoid and *effera* from a leg bone the difficulty of direct comparison between the two is obvious. The assumption that the Agate Quarry bird is congeneric with the species from the Loup Fork of Phillips County, Kansas, is arbitrary and is based solely upon the finding that both species concerned belong in the Milvinae. Since the two come from horizons widely separated in time it is questionable whether the relationship between them was truly generic, but for convenience they may be so united for the present.

Three toe joints are mounted in place on the block that contains the metatarsus of this species. The fourth toe is represented by the basal phalanx only. This, shorter and heavier than in modern Milvinae, is 5.5 mm. long. The basal phalanx of the middle toe measures 11 mm. and the second phalanx of the same digit 7.5 mm. These offer no peculiarities other than those noted.

#### BUTEONIDÆ INDETERMINATE

The proximal end of a right ulna (No. 466, collection of Harold J. Cook) taken in April, 1922 from Lower Miocene deposits at the same locality as that worked by the American Museum party in 1921 represents a hawk about as large as a caracara (*Polyborus*). The bone is considerably worn, but seems to have a very low carpal ridge. It is faintly suggestive of *Milvago chimango* but is much larger.



## BUTEONIDÆ INDETERMINATE

The lower end of a right metatarsus (Princeton University Geological Museum Cat. No. 12157) collected by Dr. W. J. Sinclair at his locality 1000 D (in T. 25 N., R. 54 W., N. E.  $\frac{1}{4}$  of Sec. 2) belongs to a hawk of the family Buteonidæ that may not at present be definitely determined. Dr. Sinclair informs me that this bone was secured with a few remains of a deer *Merycodus* (cf. *necatus*) from unconsolidated sand, apparently of the Upper Miocene level, though the fossils secured are too scanty to determine that point definitely. It is unfortunate that this specimen is not more complete since in many ways it is one of the most interesting in the entire collection studied in the present paper. The fragment consists of the lower part of a metatarsus with outer and inner trochleæ broken away and the middle trochlea considerably worn. It is peculiar in that the shaft on both anterior and posterior surfaces is flattened so that the support upon which the trochleæ rest is almost plane, instead of being depressed posteriorly at the base of the inner trochlea as is true in a vast majority of the genera of birds. In addition, the articular facet for the first metatarsal is placed very low on the shaft. Though broken, and somewhat worn the bone does not appear to have been flattened by crushing, nor does it seem to be deformed.

The fragment available is suggestive of the marsh hawks (*Circus*) and the bird hawks of the genera *Accipiter* and *Astur*, while in the low position of the facet for the first metatarsal it is similar to the carrion hawks (*Polyborus*, *Milvago* and *Ibycter*). The bone resembles that of the common marsh hawk (*Circus hudsonius*) in general sculpture, and in its broadened median trochlea with a distinct excavation at its base on the posterior surface, but is somewhat more robust, is more flattened at the distal end of the shaft, and has the first metatarsal articulation lower. *Astur* and *Accipiter* have the same flattened shaft and similar ridges to the fossil, but have the median trochlea narrower and the first metatarsal articulation higher. The fossil resembles these in the angular form of the internal intertrochlear sulcus, which is V-shaped, sloping outward to the base of the internal trochlea, rather than U-shaped as in *Circus*. The fossil is not near the group containing *Buteo* though placed there in preliminary examination (see 1915, Proc. Amer. Phil. Soc., LIV, p. 77).

The bone under discussion may be representative of a primitive stock ancestral to some of our modern forms; additional remains will be awaited with interest, as it is felt that the present specimen is too fragmentary to warrant a name.







**Article XIII.**—FURTHER NOTES ON THE MOLARS OF *HESPEROPITHECUS* AND OF *PITHECANTHROPUS*

BY WILLIAM K. GREGORY AND MILO HELLMAN

With an Appendix Entitled

NOTES ON THE CASTS OF THE *PITHECANTHROPUS* MOLARS

BY GERRIT S. MILLER, JR.

In response to our request, Dr. Gerrit S. Miller, Jr., of the U. S. National Museum, has kindly examined our manuscript and submitted a number of important suggestions and criticisms. The National Museum has also very generously loaned us for comparison a large series of upper molars of oranges, chimpanzees, and gorillas. Dr. Miller's notes and material raise again the following questions:

1.—Is the type of *Hesperopithecus* a third upper molar, as Dr. Miller is inclined to think, or is it a second upper molar as suggested in our previous paper?<sup>1</sup>

2.—With regard to arrangement and form of the roots, is the *Hesperopithecus* type more like the orang, the chimpanzee, the gorilla, or man?

3.—Of the characters revealed in the *Hesperopithecus* type can we separate those which indicate its position as a member of the man-anthropoid series from those which distinguish it from the different genera of this group?

4.—What is the homology of the paratype tooth of *Hesperopithecus*? Is it an upper or a lower molar and which molar is it?

5.—Besides these questions the problem is again raised as to the nearer resemblances and differences of the second and third molars commonly attributed to *Pithecanthropus*.

6.—Finally, is it possible that the *Hesperopithecus* molar might represent not a primate but a carnivore, as Dr. Smith Woodward is still inclined to think?

1.—IS THE TYPE OF *HESPEROPITHECUS* A SECOND OR A THIRD UPPER MOLAR?

We have been inclined to regard it as a second upper molar for the following reasons.

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<sup>1</sup>Gregory, William K., and Hellman, Milo. 1923. 'Notes on the Type of *Hesperopithecus harold-cookii* Osborn.' American Museum Novitates, No. 53.



(a.) Its extreme wear, which is unusual in third upper molars of known men and apes.

(b.) As noted in our first paper, it approaches the second upper molar of a certain chimpanzee in the transverse diameter of the posterior moiety of the crown, in the angle of the outer surface of the crown to the anterior surface, and in the degree of divergence of the axis of the lingual root to that of the anterior buccal root.

We have, however, recently noticed the cast of a very old gorilla (A. M. N. H. No. 198) in which the third upper molar is almost as much worn down as that of the type of *Hesperopithecus*. One of the gorilla third molars of the National Museum collection (No. 176212) has a contour of the crown which is less unlike the *Hesperopithecus* type than any other gorilla examined (Fig. 3). It widely differs, however, in the inclination of the occlusal surface to the axis of the palatal root (Fig. 3). In *Hesperopithecus*, if the general occlusal plane is placed in a horizontal position, the palatal root is inclined slightly forward. In this gorilla the homologous axis is inclined strongly backward, and this seems to be true of many third upper molars of various anthropoids and men. It must be admitted that the general form of the crown of one specimen and the appearance of the root of another gorilla m<sup>3</sup> approach *Hesperopithecus* and afford support to Dr. Miller's view. But, in our judgment, the wide difference in inclination of the occlusal surface to the vertical axis of the root constitutes an objection to the type of *Hesperopithecus* being a third upper molar. In these relations its most significant resemblances appear to be with the second or first upper molar of certain men (Fig. 3).

In answer to the preceding paragraph Dr. Miller replies (December 7, 1922) as follows:

I think you give undue weight and a wrong interpretation to the slant of the inner root with relation to the plane of the occlusal surface. In the third molar of gorillas I find that this slant appears always to begin by being backward, but as wear of the crown goes on it tends to work over to a forward condition which in a tooth as much worn as No. 176206 may become so like the slant in *Hesperopithecus* that I think you are wholly unjustified in placing such reliance on this feature of the fossil as your remarks on page 9 would indicate. With the third molar of No. 176206 I am sending the second [molar] tooth. Here you will see the slant of the inner root is backward instead of forward.

Our Fig. 3 shows that with regard to the point under consideration the *Hesperopithecus* type agrees with first and second upper human molars more than with the third upper gorilla molars. To this statement Dr. Miller, in turn, replies (March 14, 1923): "But the differences in this respect between one gorilla tooth and the human teeth is very much less than that between the two gorilla teeth."





Fig. 1. Series of orang third upper molars showing wide variability in size. U. S. Nat. Mus. specimens. Natural size. All but the lower right hand specimen (which is an  $m^3$  left) are third right upper molars, seen from the rear.

Upper row: U. S. Nat. Mus. Nos. 142181, 145313.

Middle row: U. S. Nat. Mus. Nos. 153807, 145300, 153820.

Lower row: U. S. Nat. Mus. Nos. 49853, 153805, 153813.



Fig. 2. Series of chimpanzee third right upper molars showing wide variability in size. Natural size.

A. M. N. H. 51394; U. S. Nat. Mus. Nos. 236977, 176235, 176240, 176241, 174710, 236971





Fig. 3. Comparison of *Gorilla*, *Hesperopithecus* and human molars.  $\times 2$ .

Upper row: Amerind  $m^2$  (A. M. N. H. T 2162);  $m^1$  of same; Amerind  $m^2$  (A. M. N. H. T 2166). Lingual view.

Middle row: *Gorilla* sp.  $m^3$  (U. S. Nat. Mus. 176212); *Hesperopithecus* type; *Gorilla* sp.  $m^3$  (U. S. Nat. Mus. 176206). Crown view.

Lower row: *Gorilla* sp.  $m^3$  (U. S. Nat. Mus. 176212); *Hesperopithecus* type; *Gorilla* sp.  $m^3$  (U. S. Nat. Mus. 176206). Lingual view.



2.—WITH REGARD TO THE ARRANGEMENT AND FORM OF THE ROOTS, IS THE *HESPEROPITHECUS* TYPE MORE LIKE THE ORANG, THE CHIMPANZEE, THE GORILLA, OR MAN?

The orang third upper molars of the National Museum series differ immensely among themselves (Fig. 1) from a very large tooth 15.7 mm. in antero-posterior length to a very small tooth only 9 mm. in length. The former differs from the *Hesperopithecus* type in having a very large hypocone and two widely separated buccal roots; the latter differs from the same in having an excessively contracted crown with greatly crowded external roots. Several of the orang molars have long straight palatal roots of subcylindrical appearance. The postero-external root in orangs tends to be double and either to diverge from or not to converge toward the palatal root.

The National Museum material (Fig. 2) indicates that in chimpanzees the palatal roots of all the third molars are usually comparatively short, pointed toward the root end, and relatively weak, while those of the gorillas are long, stout, and not sharply tapering. In this point the *Hesperopithecus* type is decidedly nearer to the gorilla.

Next, the palatal root of the *Hesperopithecus* type is deeply grooved vertically on its buccal aspect. Dr. Miller suggests that there is a resemblance here (Fig. 4) with certain gorilla third upper molars (U. S. Nat. Mus. Nos. 174713 and 176205) in which the raised posterior border of the groove is formed through the coalescence of the postero-external (distobuccal) root with the palatal root. It is hardly possible that in *Hesperopithecus* the posterior border of the deep groove in question can be formed through a similar coalescence, because the radiographs (published in our previous paper, Fig. 5) show but one canal on the palatal side, while if any part of the postero-external root were present it should show another canal, or portions of it; secondly, a coalescence of this kind assumed by Dr. Miller would not account for the similar upraised border on the antero-internal side of the palatal root, where there is no question of any coalescence. While the grooved internal border is more pronounced than in any anthropoid or human specimen examined by us, this does not necessarily mean that there was a coalescence of the postero-external root with it. In fact, we are still inclined to think that the antero-external root was free at its apex but confluent at the base with the raised border of the palatal root and that a remnant of the forking between the antero-external and the palatal root is still visible.

In reply to the foregoing Dr. Miller writes as follows:

I should not expect to find a second canal present in a tooth formed and broken in the way I suppose the type tooth to have been formed and broken. My idea will





Fig. 4. Comparison of *Gorilla*, *Hesperopithecus*, orang and chimpanzee molars. View from above showing roots.  $\times 2$ .

Upper row: *Gorilla*, U.S. Nat. Mus. No. 176212; orang, U. S. Nat. Mus. No. 142181; chimpanzee, A. M. N. H. No. 51394.

Lower row: *Gorilla*, U. S. Nat. Mus. 176206; *Hesperopithecus* type; *Gorilla*, U. S. Nat. Mus. 174716.

perhaps be made plain by the red ink on the roots of  $m^3$  in gorilla No. 176206 which I am now sending you. Here I have marked with red the entire portion of the roots that I suppose to be absent in the type. The unmarked portion of the tooth No. 176206 is naturally not exactly like the type of *Hesperopithecus* because the specimens came from representatives of different genera, but the likeness is sufficiently close to make me think that this is the most probable explanation of the type's history.

In Fig. 5 we figure on the left the two gorilla third molars, on the lower one of which Dr. Miller has marked in red the region which he supposes to be absent in the type of *Hesperopithecus*; next to this we show the type of the latter, and at the right above a chimpanzee  $m^3$  in which the postero-external root has been broken off, and below a gorilla  $m^3$  with the same root preserved and distinct from the palatal root. We are, however,





Fig. 5. Comparison of *Gorilla*, *Hesperopithecus* and chimpanzee molars. Posterior side.  $\times \frac{5}{3}$ .

Upper row: *Gorilla*, U. S. Nat. Mus. No. 176212; chimpanzee, A. M. N. H. No. 51394.

Middle row: *Hesperopithecus* type.

Lower row: *Gorilla*, U. S. Nat. Mus. No. 176206; *Gorilla*, U. S. Nat. Mus. No. 174716.

rather inclined to attribute the lack of projecting portions of this root in the type to the same extreme attrition which has smoothed down all other projections of the tooth. We still think that a small portion of the place where the postero-external root forked away from the base of the pulp cavity may be seen; also that the resemblance between the anterior and posterior ridges flanking the median groove is too close for them to have been formed in one case by coalescence with the postero-external root, and in the other case not so. In other words, the evidence suggests to us that the postero-external root was divergent as in certain chimpanzees, gorillas and men (Fig. 5).



The buccal groove on the palatal root, while deeper than in any other tooth we have seen, is feebly developed in certain orang, gorilla, and chimpanzee teeth (Fig. 4).

In short, in the arrangements and form of the roots the *Hesperopithecus* characters are distributed as shown in Table 1.

TABLE I.—COMPARISON OF THE ROOTS

|                                                                                           | <i>Hespero-<br/>pithecus</i> | Orangs | Chimpan-<br>zees | Gorillas | <i>Pithecacanthropus</i> | Men                      |
|-------------------------------------------------------------------------------------------|------------------------------|--------|------------------|----------|--------------------------|--------------------------|
| Forward (+) Intermediate (0) Backward (—) Inclination of Palatal Root to Occlusal Surface | +                            | —      | —                | —        | —                        | O<br>—<br>+ <sup>1</sup> |
| Palatal Root Deeply Grooved on Palatal Side                                               | —                            | +      | +                | +        | —                        | —                        |
| Palatal Root Deeply Grooved on Buccal Side                                                | +                            | +      | Usually weak     | +        | —                        | —                        |
| Relative Antero-posterior Diameter of Lingual Root                                        | +                            | +      | —                | ++       | +                        | +                        |
| Divergence of Lingual Root from External Roots                                            | +                            | —      | +                | +        | +                        | +                        |
| Relative Transverse Width of Antero-external Root Compared with Palatal Root              | —                            | +      | —                | +        | ++                       | ++                       |
| Divergence (+) or Confluence (—) of Postero-external with Palatal Root                    | +                            | +      | +                | +        | +                        | +                        |

This shows the distribution of agreements and disagreements of root characters to the best of our judgment.

3.—CAN WE SEPARATE THOSE CHARACTERS WHICH INDICATE THE POSITION OF *HESPEROPITHECUS* AS A MEMBER OF THE MAN-ANTHROPOID SERIES FROM THOSE WHICH DISTINGUISH IT FROM THE DIFFERENT GENERA OF THIS GROUP?

(a.) The members of the group tend to have an asymmetrical molar crown, but in the anthropoids the transverse diameter of the posterior moiety as compared with that of the anterior moiety is relatively smaller than in modernized man. In this character the type of *Hesperopithecus* conforms rather with anthropoid than with modernized human conditions; but not too much weight should be given to this

<sup>1</sup>The variability is probably revealed by the more abundant material in comparison with that available in the other groups.



character because the enamel shell which covers the outside of the crown is lost in *Hesperopithecus* and this, if present, would alter considerably the appearance of the outer side of the tooth. The resemblances of the crown, as shown in Index 1 of our previous paper, are rather with chimpanzee molars than with human molars.

(b.) The great width and flatness of the lingual root distinguish *Hesperopithecus* from the chimpanzee and approach the condition in the gorilla, but in *Hesperopithecus* the palatal surface of the palatal root has at most a very slight vertical groove, while in the gorillas this groove is very large and deep.

(c.) In *Hesperopithecus* the transverse diameter of the antero-external root is moderate as compared with the excessive width of this root in man (some gorillas distinctly approach the human condition in the wide transverse diameter of the antero-external root and in the relatively small transverse diameter of the palatal root). In exhibiting the opposite of these characters *Hesperopithecus* is somewhat nearer to the chimpanzee.

(d.) The radiographs, aside from showing that the roots and pulp cavity of *Hesperopithecus* conform to the general man-anthropoid type, do not appear to reveal any clear-cut generic characters.

In brief, the more important characters of the *Hesperopithecus* type, the combination of which in one specimen may prove to be generic, are as follows:

(a.) Relative antero-posterior diameter of crown of  $m^2$  (?) greater than in men and less than in apes.

(b.—Assuming that the *Hesperopithecus* type is an  $m^2$ .) The small size of the hypocone, contrasting with nearly all anthropoids and all primitive men.

(c.) The more vertical relation of the palatal root to the worn occlusal surface, most nearly approached in certain human teeth.<sup>1</sup>

(d.) The deep groove on the buccal side of the palatal root, deeper than any observed in apes or men.

(e.) Palatal root probably longer than in men excepting certain Indian teeth and approaching gorilla type.

(f.) Transverse diameter of antero-external root relatively smaller than in men and larger than in chimpanzees.

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<sup>1</sup>Dr. Miller writes: "Yes, but your Fig. 3 shows that the difference between *Hesperopithecus* and one gorilla is very much less than that between two gorillas."



#### 4.—HOMOLOGY OF THE SECOND SPECIMEN REFERRED TO *HESPEROPITHECUS*

The second specimen (A. M. N. H. No. 17736) of Professor Osborn's original description (*op. cit.*, p. 4) is excessively worn and eroded (Fig. 6) but after prolonged comparisons we are inclined to accept Professor Osborn's provisional determination of it as a third right upper molar. In the contour of the base of the crown it somewhat resembles the third upper molar of a certain chimpanzee (A. M. N. H. No. 51394) but very probably had a longer palatal root.

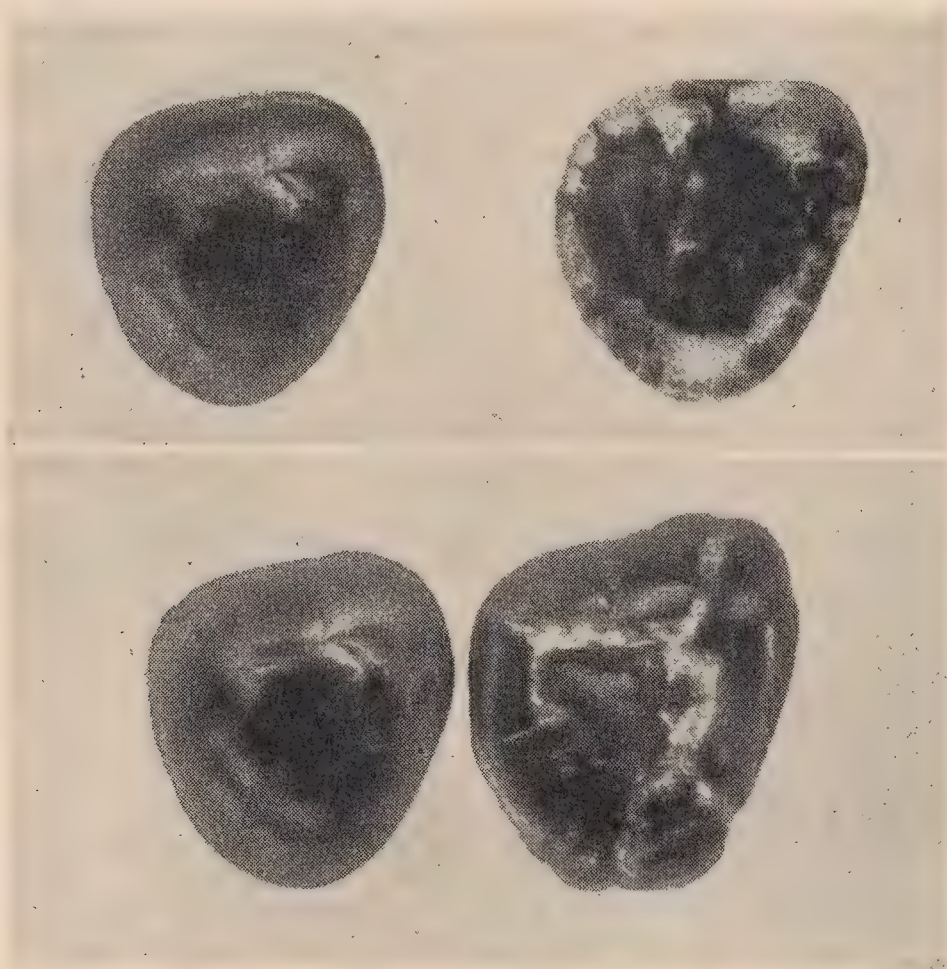


Fig. 6. Second specimen, or paratype, of *Hesperopithecus haroldcookii* compared (upper pair) with  $m^3$  of a chimpanzee and with (lower pair) the type.

#### 5.—*HESPEROPITHECUS* AND *PITHECANTHROPUS*

In our preliminary report on the *Hesperopithecus* molar as cited by Professor Osborn (*op. cit.*, p. 2) we stated that "On the whole we think its nearest resemblances are with *Pithecanthropus* and with men rather than with apes." One of us (M. H.) is still inclined toward this view, while to the other (W. K. G.) it appears that, apart from the relation of the occlusal plane to the palatal root, the prevailing resemblances of the *Hesperopithecus* type are with the gorilla-chimpanzee group.

In our first report we cited the evenly concave wearing surface as a point of resemblance to *Pithecanthropus*. This form of extreme wear is quite common in Indians and Australians, but we have also found it in



a single gorilla (represented by a cast, A. M. N. H. No. 198) while Dr. Miller informs us that he finds a similar condition in a chimpanzee (U. S. Nat. Mus. 174700) also. Hence this character can hardly be taken as diagnostic.

As we recognized at first, the *Hesperopithecus* molar could hardly have supported a hypocone as large as that of the *Pithecanthropus* m<sup>2</sup>; it differs also in the transverse narrowness of the antero-external root and in the much smaller antero-posterior diameter of the palatal root.



Fig. 7. Comparison of *Pithecanthropus*, Australian and orang molars.  $\times 2$ .

Upper row: Third right upper molar (cast) referred to *Pithecanthropus*; m<sup>3</sup>, right, of Australian aboriginal (A. M. N. H.); m<sup>3</sup>, right, of orang, U. S. Nat. Mus. 153805.

Lower row: Second left upper molar (cast) referred to *Pithecanthropus*, m<sup>2</sup>, left, of Australian aboriginal (A. M. N. H.).

If the second specimen of *Hesperopithecus* be rightly regarded as an extremely worn m<sup>3</sup> (see above), then the differences of *Hesperopithecus* from *Pithecanthropus* become more emphatic, because the section of the base of the crown of the "second specimen" of *Hesperopithecus* had a prominent postero-external and reduced postero-internal angles and its



crown was relatively long antero-posteriorly and narrow transversely, while the opposites of these features characterize  $m^3$  of *Pithecanthropus*.

The nearer resemblances of the second and third upper molars referred to *Pithecanthropus* appear (Figs. 7, 8) to be rather with the corresponding molars of Australians than with those of apes.<sup>1</sup> They are



Fig. 8. Comparison of *Pithecanthropus*, Australian and orang molars. Same specimens as in Fig. 7. Posterior (distal) view.  $\times 2$ .

much larger than those of most Australian aborigines (though smaller than those of the Talgai skull), and have much heavier and more divergent inner and outer roots. The third upper molar differs from the Australian here figured in having a less protuberant hypocone, while in the second upper molar the relative length of the antero-posterior as compared with the transverse diameter is much greater.

<sup>1</sup>Dr. Miller writes: "This statement seems to me much too strong in view of the variation in crown form shown by apes. See especially the orang teeth ( $m^2$ ) left row sent" (Figs. 14, 15). On this point see the Appendix, below.



6.—*HESPEROPITHECUS* NOT A CARNIVORE

Dr. Smith Woodward still doubts that the type molar of *Hesperopithecus* belongs to a primate and inclines to regard it as one of the primitive extinct bears (*Hyænarcos*).<sup>1</sup> Dr. Matthew, who has had exceptionally long and wide experience in studying the teeth of fossil and recent carnivores, has endorsed the judgment of Professor Osborn that the tooth is not that of a carnivore. One of us (W. K. G.) has repeatedly searched the Museum collections of carnivores for further evidence bear-



Fig. 9. Upper molars of modern carnivores. Distal, or rear, view.  $\times 2$ .

Upper row: *Bassaricyon osborni* m<sup>2</sup>, A. M. N. H. No. 32609; ditto, m<sup>1</sup>; *Cercoleptes (Potos) flavus* m<sup>1</sup>, A. M. N. H. No. 15475; ditto, m<sup>2</sup>.

Middle row: *Nasua* sp. m<sup>3</sup>, A. M. N. H. No. 35453; ditto, m<sup>2</sup>; *Viverra zibettha* m<sup>1</sup>, A. M. N. H. No. 91.

Lower row: *Ælurus fulgens*, m<sup>1</sup>, A. M. N. H. No. 32650; *Procyon lotor*, m<sup>2</sup>, A. M. N. H. No. 8335; *Mephitis* sp. m<sup>1</sup>, A. M. N. H. No. 77.

ing on the problem. First, comparing the *Hesperopithecus* type with carnivores in general, we find: (1) In the upper molars of carnivores of all known families the vertical distance from the middle of the occlusal surface to the bottom of the pulp cavity, where the inner and outer roots fork, is proportionately much less than in *Hesperopithecus* (Figs. 8, 9, 13).

<sup>1</sup>Nature, November 25, 1922, CX, p. 707.



In other words, the latter molar is not nearly so brachyodont, but has a vertically deeper pulp cavity, as in apes and men, its apparent brachyodonty being due both to extreme natural wear and to the rounding and attrition of the enamel borders. (2) In typical carnivores (Fig. 9) the two outer roots are relatively slender and separated widely from each other and from the inner root. (3) The antero-external root is usually narrower transversely, less compressed antero-posteriorly, and more conical than



Fig. 10. Upper molars of modern carnivores. Viewed from above, showing roots.  $\times 2$ . Same specimens as in Fig. 9.

in *Hesperopithecus*. (4) The palatal, or inner, root of carnivores is often more widely divergent from the outer roots, is not flattened on the palatal surface, is not deeply grooved on its buccal side and is relatively shorter and more pointed apically. (5) In these carnivore molars which have a hypocone it juts obliquely backward and inward, and the crown at its base is relatively wider than in *Hesperopithecus*.

Secondly, comparing the *Hesperopithecus* type molar with those of *Hyænarcos* and other ursids (Figs. 11, 12, 13), we find that some of the modern ursids depart from the normal carnivore type described above, in the following respects: (1) The palatal root (Fig. 12) becomes excessively wide, far wider than in *Hesperopithecus*, and (2) it exhibits a





Fig. 11. Comparison of *Hesperopithecus* molar with *Hyænarctos* and other ursoid carnivore molars. Occlusal view.  $\times \frac{4}{3}$ .

Upper row: *Amphicyon sinapius*, A. M. N. H. No. 18259, Lower Snake Creek beds (Upper Miocene); *Ursus malayanus*, A. M. N. H. No. 296.

Middle row: *Hesperopithecus* type. Upper Snake Creek beds (Lower Pliocene).

Lower row: *Indarctos* (?) sp., Upper Snake Creek beds (Lower Pliocene), Coll. H. J. Cook; *Hyænarctos gregoryi*, Univ. Calif. No. 24025, Eden beds (Pliocene).

tendency to divide into anterior and posterior moieties; (3) as a consequence, the buccal side of the palatal root exhibits a prominent vertical groove; (4) at the same time the antero-external (mesio-buccal) root becomes widened transversely. But these points of partial agreement, either with *Hesperopithecus* or with other anthropoids, are at once seen to be analogies and not homologies indicative of close relationships, first, by reason of the wide dissimilarity of the ursid and *Hyænarctos* molar crowns to that of *Hesperopithecus* and other anthropoids and, second, because the *Hesperopithecus* molar crown and roots differ totally from the PRIMITIVE carnivore types as described above, while the ursid and *Hyænarctos* crowns and roots are as clearly derived from it.





Fig. 12. Comparison of *Hesperopithecus*, *Hyænarcos*, etc. (continued). Same specimens as in Fig. 11, viewed from above.  $\times \frac{4}{3}$ .

In conclusion, the profound differences of the *Hesperopithecus* tooth from that of carnivores throws into stronger relief its numerous and fundamental points of agreement with those of the ape-man group of the primates.

#### CONCLUSIONS

1.—The question whether the type of *Hesperopithecus* is a third upper molar or a second is still open but we incline to the view that it is a second.

2.—The greater number of resemblances of the type appear to be with gorilla and chimpanzee rather than with orang. One of us (M. H.) still regards the human resemblances as being of considerable signifi-





Fig. 13. Comparison of *Hesperopithecus*, *Hyænarcos*, etc. (continued). Same specimens as in Figs. 11 and 12. Mesial or anterior view.  $\times \frac{4}{3}$ .

cance, while the other (W. K. G.) leans toward the anthropoid affinities of the type. The range of variability in crown and root characters of the molars both in the Hominidæ and the Simiidæ is so great and so overlapping as to warrant either interpretation.

3.—In view of the foregoing, the exact generic diagnosis of *Hesperopithecus* must await further discoveries.

4.—The paratype, or second specimen, of *Hesperopithecus* is pretty surely an upper molar and is probably a third.

5.—The second and third upper molars found near the *Pithecanthropus* skull top approach those of an Australian aboriginal here figured, but are even closer to those of certain oranges selected by Doctor Miller (see Appendix), especially in the roots. We cannot, however, accept



unreservedly his conclusion that the teeth referred to *Pithecanthropus* are probably those of a now extinct Javan great ape, representing the orangs of Sumatra and Borneo. Striking as these resemblances are, the fact should not be dismissed that the third molar was found in apparent association<sup>1</sup> with a cranium and femur of unquestionably human, or subhuman, type, and in the lack of additional evidence we think it profitless to assume that the teeth do not belong with the skull. The peculiar contraction of the occlusal surface and the orang-like crenation of the enamel of the *Pithecanthropus* m<sup>3</sup> is well shown in the molars of a certain Bantu negro (A. M. N. H. No. D 7), while other features (jutting hypocone, sloping ectoloph, etc.) may be matched in other human teeth.

6.—Professor Osborn's determination of the type of *Hesperopithecus* as a new genus of anthropoid apes has not been universally accepted. The following possible identifications of the type have been made by various persons.

(1) Upper molar of an anthropoid ape, probably a new genus (American Museum staff).

(2) Lower molar of *Hyænarctos* or allied genus of ursid.

(3) Upper molar of the same.

(4) A "bear's tooth."

(5) A molar of an otherwise wholly unknown type of carnivore.

(6) An upper or lower molar of some carnivore allied with *Æluropus*.

(7) An upper molar of a gigantic relative of the procyonid carnivore *Potos*.

(8) An upper molar of a gigantic relative of such South American monkeys as *Pithecia* and *Lagothrix*.

(9) The first upper deciduous premolar of a Pliocene horse.

(10) An incus bone of a gigantic mammal.

We have considered each of these with unbiased minds and compared the type with the various specimens suggested, as well as with many others, but have returned with more confidence to the conclusions set forth above (Nos. 1 to 4).

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<sup>1</sup>According to Dubois (1894, pp. 2, 3) the calvarium was found only one meter distant from the site of the third molar and in the same plane. In this connection Dr. Miller writes: "In publishing anything about the Javan teeth I particularly wish to avoid all discussion of the bones. The latter I have never examined critically, and I have so many other things on hand that I do not wish to become interested in a subject which I can foresee would be more than absorbing. About the teeth, however, I am very glad to place my opinion on record."



APPENDIX.—NOTES ON THE CASTS OF THE *PITHECANTHROPUS* MOLARS<sup>1</sup>

BY GERRIT S. MILLER, JR.

Whatever the bones may prove to be, I think that the molars referred to *Pithecanthropus* are probably those of a now extinct Javan great ape representing the orangs of Sumatra and Borneo. Whether or not this ape was strictly congeneric with the orangs I am not prepared to say, because the teeth, like those of *Hesperopithecus*, are neither in sufficiently good condition nor in sufficiently great number to show what the animal's dental characters really were; but, so far as they go, they come almost within the limits of individual variation of the living orangs, and in the slight peculiarities where they differ from orangs they do not approach men. Hence I think it is entirely misleading to speak of your fossil as showing resemblances "with *Pithecanthropus* and men rather than with apes" (your p. 12).

Here is my evidence and I shall be interested to know what you think of it.

(a.) The Second Upper Tooth.—Compare the cast with orangs (Fig. 14 *a-d*) Nos. 142170 (*a*), 142197 (*b*), 145304 (*c*), and 153808 (*d*). These four specimens seem to me to cover all the essential features of the cast. They show more tendency for the crown to swell out beyond the level of the roots along the anterior border, and less to swell out in the region of the hypocone; but I should hesitate to regard this as anything more than an individual character unless it were known to be constant in many teeth. The peculiar form of the roots in the cast is very nearly duplicated in No. 145304 (Fig. 15 *a, i*). Notice in this connection the striking difference in root form which exists between Nos. 145304 (Fig. 15 *a, i*), and 142197 (Fig. 15 *c, k*); it is much greater than that between 145304 and the cast (*b, j*). The other specimens (Fig. 14 *e-k*) are sent to show the range of variation in m<sup>2</sup>. Compare 153822 (Fig. 14 *g*) and 142185 (Fig. 14 *e*) for difference in length-breadth ratio; 142197 (*b*) and 153816 (*h*) for difference in size of two males; 153822 (*g*) and 142185 (*e*) for difference in development of hypocone (that this is not a sexual character is shown by the large hypocone in No. 153824 (*j*)); Nos. 153808 (*d*) and 153822 (*g*) for difference in development of paracone and metacone and of the sulcus between them; No. 145322 (*q*) for a peculiar narrowing of the area of wrinkled enamel. After examining all of these

<sup>1</sup>Excerpts from two letters from Gerrit S. Miller, Jr. to W. K. Gregory; published here with Dr. Miller's kind permission. The orang molars illustrated in Figs. 14, 15 were loaned by the U. S. National Museum. For these courtesies and for Dr. Miller's unfailing coöperation the authors desire to express their gratitude.





Fig. 14. Comparison of *Pithecanthropus* and orang molars. Occlusal view,  $\times \frac{3}{2}$ . Second upper molars:

*a*—U. S. N. M. 142170; *b*—142197; *c*—145304; *d*—153808; *e*—142185; *f*—*Pithecanthropus*; *g*—153822; *h*—153816; *i*—49856; *j*—153824; *k*—145307.

Third upper molars:

*l*—142191; *m*—142169; *n*—*Pithecanthropus*; *o*—153806; *p*—142181; *q*—145322.



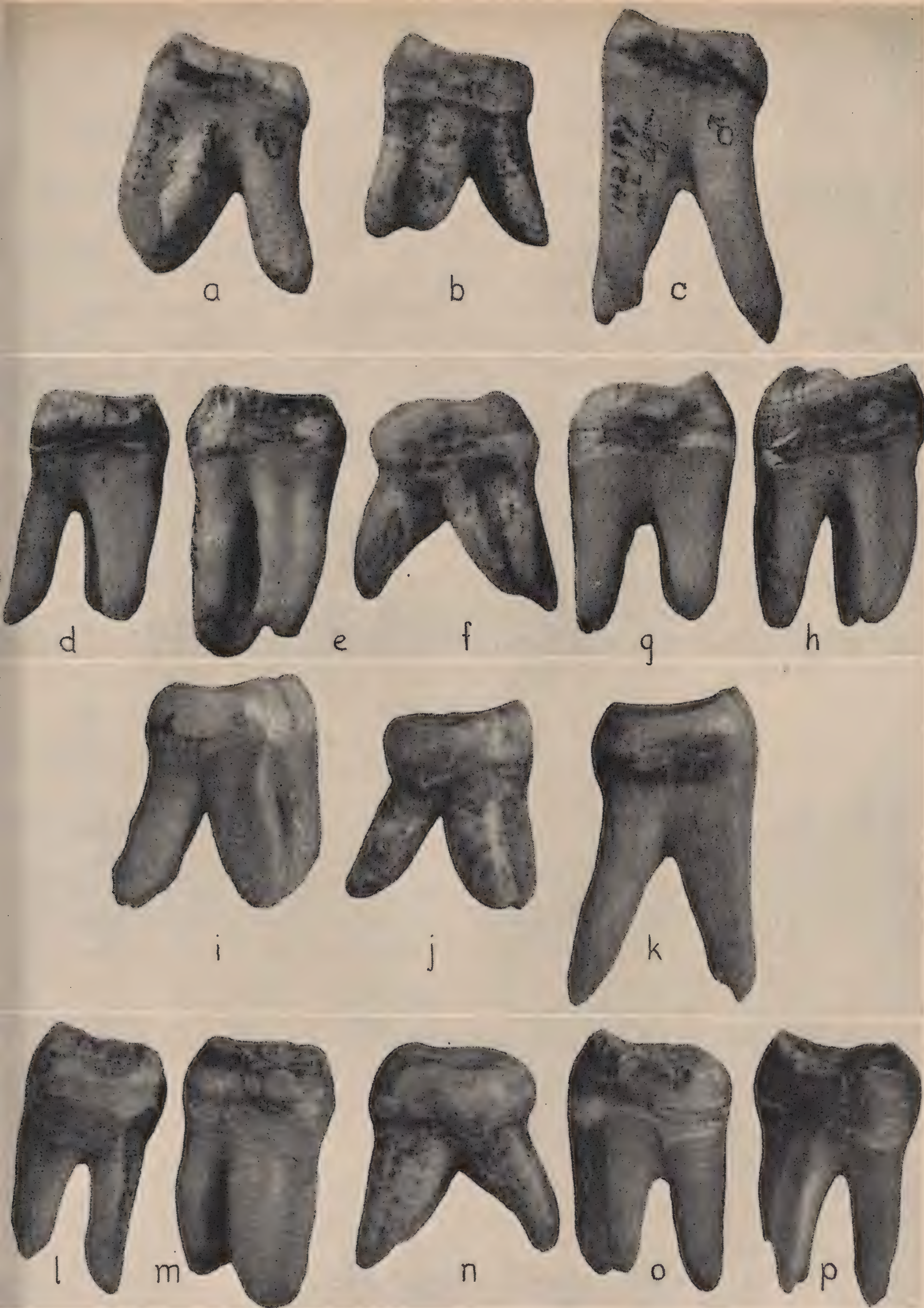


Fig. 15. Comparison of *Pithecanthropus* and orang molars continued.  $\times \frac{3}{2}$ .

Anterior view, second upper molar:

a—145304; b—*Pithecanthropus*; c—142197.

Anterior view, third upper molar:

d—142191; e—142169; f—*Pithecanthropus*; g—153806; h—142181.

Posterior view, second upper molar:

i—145304; j—*Pithecanthropus*; k—142197.

Posterior view, third upper molar:

l—142191; m—142169; n—*Pithecanthropus*; o—153806; p—142181.



can you show me any character in the cast that you would be willing to call generic on the basis of one tooth?

(b.) The Third Upper Tooth. (Fig. 14 *l-p*).—Compare the cast (Fig. 14 *n*) with Nos. 142169 (*m*) and 142191 (*l*) and especially 153806 (*o*) for near approach in crown outline; then compare these three orangs with No. 142181 (*p*) in order to realize how much the third molar varies in the living animal. It seems to me that the crown of the cast is easily interpreted as an orang tooth with the general form of No. 153806 (*o*) plus a slight tendency toward reduction of the wrinkled area like that shown by  $m^2$  No. 145322 (Fig. 14 *q*). The roots are not quite so easily dealt with. I cannot find any recent specimen in which they exactly agree with those in the cast, particularly as regards their angle of divergence; but in No. 142191 (Fig. 15 *l*) the two outer prongs are partly joined, and this process would need to be carried only a little farther (as the joining of the postero-external with the lingual is carried in No. 142169 (Fig. 15 *m*) to produce the conditions seen in the cast.

SUMMARY.—The only characters shown by the casts that appear to be outside of the limits of individual variation in our series of recent orangs are: (*a*) in both teeth a tendency for the posterior side of the crown to bulge out beyond the level of the roots (nearly realized in 145322); (*b*) in  $m^2$  the absence of this tendency to bulge outward along the anterior margin; and (*c*) in  $m^3$  the wider angle of divergence of the roots. These differences point to a probable specific distinctness of the extinct Javan ape from the living ones of Borneo and Sumatra; but would you be willing to regard them as of generic importance when you do not know that they are actually constant in the extinct species; or do you find some important characters in the casts that I have overlooked; or can you point out any definitely human suggestions in any of the features of the casts? In all this discussion we must keep in view the fact that it is only with casts of the *Pithecanthropus* molars that we are now dealing; the actual teeth may show features which will cause us to change our minds.



Article XIV.—THE SCALES OF THE CYPRINID GENUS  
*BARILIUS*

By T. D. A. COCKERELL

PLATE XVIII

In American Museum Novitates, No. 57 (1923), Mr. J. T. Nichols described an interesting fish from West Africa as *Barilius engrauloides*. He remarked that the origin of the dorsal fin was unusually far back, and the fish seemed more or less intermediate between *Barilius* and *Engraulicypris*. This made me wish to see the scales of *B. engrauloides*, and Mr. Nichols has very kindly sent a couple from the type specimen, one a lateral line scale, the other from just below it, over the ventral fin. The scales of this fish may be described thus:

Length slightly over 3, width about 3.5 mm.; apex broadly rounded; base moderately convex, subtruncate, with obtuse but evident lateral corners; apical radii about 9, delicate, widely spaced; basal radii one or two, short and rudimentary; nucleus about one-third length of scale from base; apical circuli parallel with margin, fine and dense; lateral circuli vertical, much more widely spaced than apical, not continuous with apical, but no distinct interval between the two sets; basal circuli more crowded than lateral, but continuous with them.

This is a genuine *Barilius* scale and is quite distinct from that of *Engraulicypris*. The type of *Engraulicypris* is *pinguis* Günther (= *sardella* Günther), a peculiar elongated fish from Lake Nyassa and Upper Shiré. The lateral circuli are widely spaced and essentially transverse, with a very wide space between them and the closely placed apical circuli; the latter, if prolonged, would cut them almost at right angles. The scales are thin and easily deciduous.

With this genus Boulenger unites *Neobola*, which is represented by several species of more ordinary looking fishes, with the mouth extending more or less below the eye. In *N. argentea* Pellegrin, the scale is extremely broad, and the lateral circuli are subvertical, yet fail to meet the apical ones. The apical radii are obsolete, whereas they are well developed in *Engraulicypris sardella*. My *N. argentea* is from Bugala, Lake Victoria (Brit. Museum). The type of *Neobola* is *N. bottegi* Vinciguerra, a species with remarkably long pectoral fins. Apparently *Neobola* is a valid genus, but it is not certain that *N. argentea* is entirely congeneric with the type. Unfortunately, the scales of the type species are not available. For the present, the two species just cited, and also



*brevianalis* Boulenger and *minutus* Boulenger, may be referred to *Neobola*, leaving *sardella* as the exponent of *Engraulicypris*. Furthermore, *Engraulicypris congicus* Nichols and Griscom, 1917, will stand as *Neobola congica*.

So far as the scales go, *Barilius vagra* Hamilton-Buchanan, belonging to the subgenus *Shacra* Bleeker (with 4 barbels) and *B. barila* Hamilton-Buchanan, belonging to the subgenus *Bendilisis* according to Day (with two barbels) are strictly congeneric. *B. vagra* has weak basal radii, but in *B. barila* these are nearly or quite obsolete. As a matter of fact, the type of *Bendilisis* Bleeker is not *B. barila* but *B. bendelisis* Hamilton-Buchanan, and on this latter basis the subgenus has some standing, on account of the spotted scales, which are quite broad and have the apical radii strong and spreading. If *Shacra* and *Bendilisis* are regarded as inseparable, the former has priority of place. The African species and also several of the Asiatic have lost the barbels. *Barilius barila* is not only to be excluded from *Bendilisis*, but it is actually the type of the genus *Barilius* Hamilton-Buchanan. The barbels are small and the African species are in general quite congeneric.

A really distinct subgenus or genus is represented by *B. andersoni* from Yunnan Fu, and *B. polylepis* from Tongchuan Fu, Yunnan, both collected by J. Graham (Brit. Museum). In these the lateral circuli are continuous with the apical ones, and all are widely spaced. The scales are broad, and only apical radii are developed. The basal corners are very obtuse or quite obsolete. For this group the name **Anabarilius** (type *andersoni*) may be appropriate. The two species were described by Regan in 1904. The subgenus *Raiamas* Jordan (*Bola* Günther), for *Barilius bola* Hamilton-Buchanan, belongs according to Day to the same group (which he wrongly calls *Barilius* s. str.) as *B. bakeri* Day, which is the type of *Pteropsarion* Günther. These fishes are, however, differently marked, and differ very greatly in the number of scales in lateral line. The character of the scales is unfortunately unknown, but I have scales of *B. tileo* Hamilton-Buchanan, which seem to be strictly congeneric with *B. bola*. In *B. tileo* the scales are about as broad as long, of a perfectly ordinary *Barilius* type with six apical radii and rudimentary basal ones. *B. tileo*, as seen by me, had the upper row of spots along the side considerably larger than the lower, the lower spots being very small. In *B. bola* this difference does not obtain.



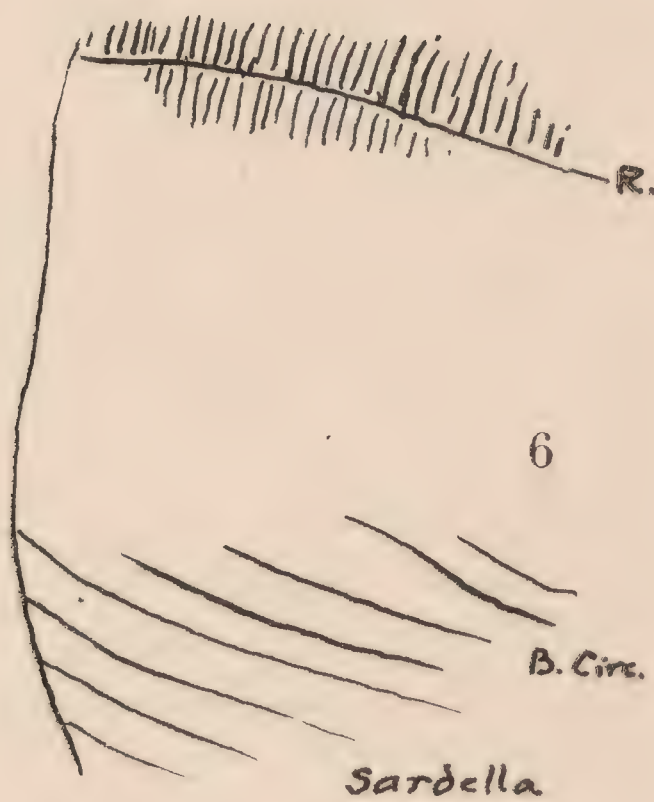
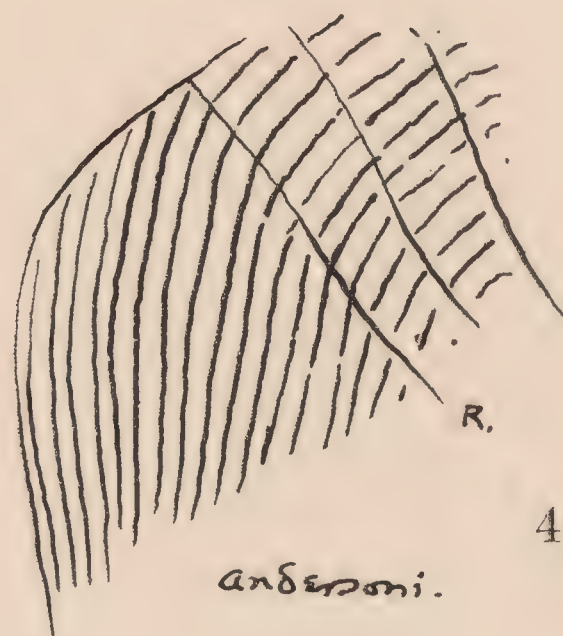
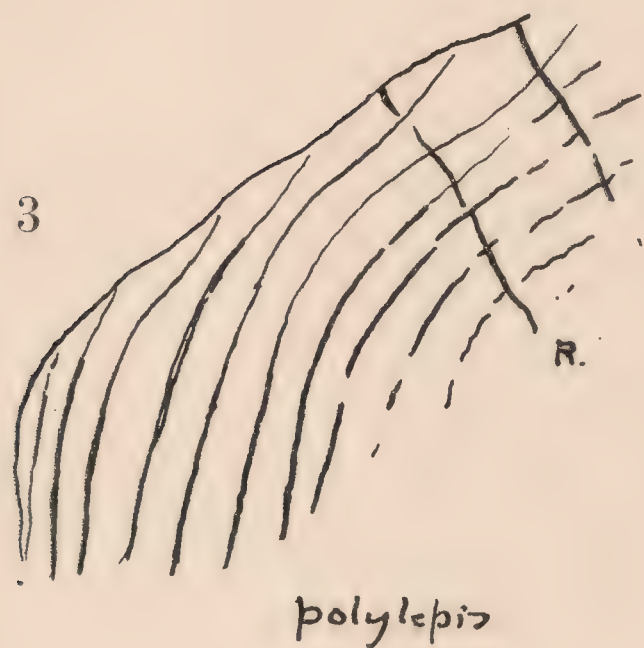
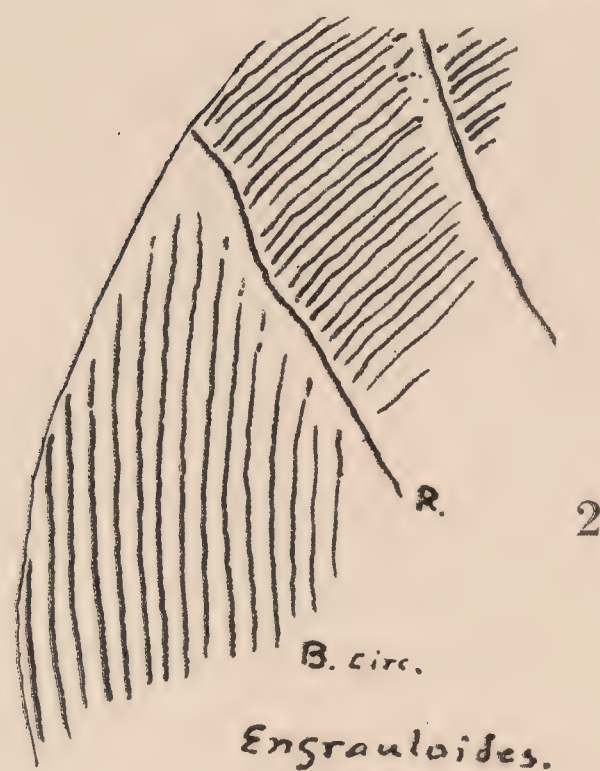
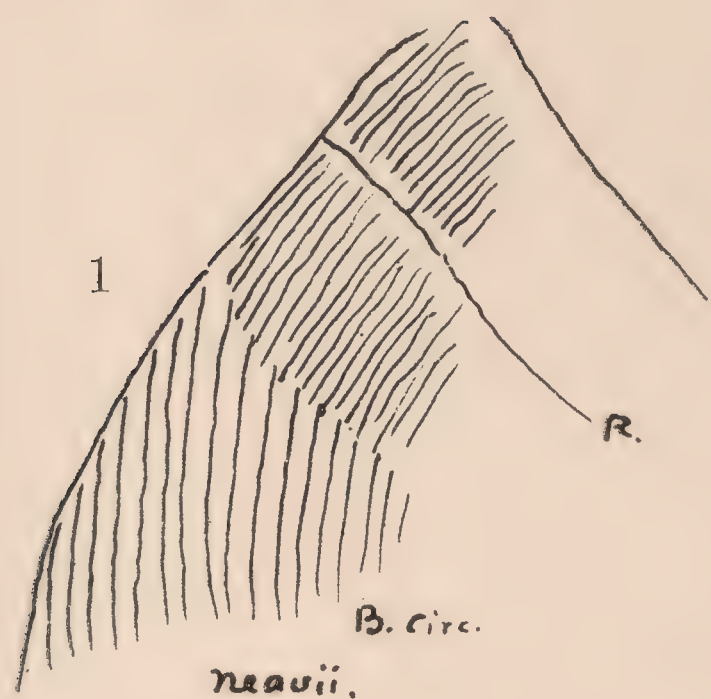
PLATE XVIII



Parts of sides of scales, to show relation of lateral (laterobasal; *B. circ.*) and apical circuli, the latter between or beyond the radii (*R.*).

- Fig. 1. *Barilius neavii* Boulenger.
- Fig. 2. *Barilius engrauloides* Nichols.
- Fig. 3. *Barilius (Anabarilius) polylepis* Regan.
- Fig. 4. *Barilius (Anabarilius) andersoni* Regan.
- Fig. 5. *Neobola argentea* Pellegrin.
- Fig. 6. *Engraulicypris sardella* Günther.











# Article XV.—CROCODILIAN PELVIC MUSCLES AND THEIR AVIAN AND REPTILIAN HOMOLOGUES

BY ALFRED S. ROMER

PLATES XIX TO XXV

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## INTRODUCTION

The pelvic musculature of the Crocodilia is of especial interest because of its bearing on the evolution of the "Archosauria." The structure of the pelvis is one of the most characteristic features of this great reptilian group, which includes the dinosaurian orders and the flying reptiles amongst others, and from which the birds are descended. Von Huene (1908) and Gregory and Camp (1918) have attempted to use the crocodilian musculature in the restoration of that of the dinosaurs. Their efforts have been hindered because of our inadequate knowledge of the anatomy of the pelvic region in these, the only living Archosauria.

Following Buttmann (1826), Stamnius (1854), Gorski (1854), Houghton (1865 and 1868), and Hair (1868), Gadow (1882) has given a description of the crocodilian pelvic musculature which has found wide acceptance. But, while it is accurate in its description, its value is lessened by the fact that it is inadequately illustrated, rendering it difficult of comprehension to those who are not familiar with the material, and more especially because of the fact that the muscles described are often obviously non-homologous with those in more typical reptiles to which the same names are applied.

The purpose of the present paper is to give a restudy of crocodilian pelvic musculature, with more adequate illustration and with a critical discussion of the homologies of the muscles concerned with those of typical reptiles (lizards and *Sphenodon*) and of birds. The system of reptilian muscle nomenclature used by the writer in a previous paper (1922) and founded mainly upon that of Gadow is followed.



From the fact that Gadow's homologies are disputed in many cases it might be inferred that I am attempting to question the value of Gadow's paper of 1882. Nothing, however, would be further from the truth, as should be obvious from the fact that in this and previous papers I have used Gadow's work as a foundation. But in attempting, as Gadow did, to homologize for the first time the pelvic muscles of all the Reptilia, it is only natural that a certain amount of error should have crept in.

In the discussion of innervations, the division into crural, obturator and sacral regions, previously adopted by the writer (1922) is followed.

The illustrations are from dissections of a young specimen of *Alligator mississippiensis*.

The antero-ventral bone of the girdle is called the pubis in this paper; its homologies are not discussed.

I wish to acknowledge my indebtedness in many ways to Dr. W. K. Gregory, at whose suggestion this work was undertaken. Dr. J. P. Chapin loaned the writer his sketches of a dissection of the pelvic region of the ostrich, which were very useful in the consideration of bird musculature. Dr. G. K. Noble, Curator of Herpetology, kindly furnished me with material for dissection.

#### DESCRIPTION OF CROCODILIAN PELVIC MUSCLES

##### DORSAL MUSCLE MASS: DORSALIS TRUNCI, DORSALIS CAUDÆ

The dorsal musculature, into the subdivisions of which it is unnecessary to enquire for our purposes, runs posteriorly above the lumbar transverse processes and then, after finding surfaces of insertion and origin on the dorsal surfaces of the sacral vertebræ and the inner dorsal portion of the ilium, continues posteriorly without interruption as the *dorsalis caudæ* between spines and transverse processes of the caudal vertebræ.

ANTERIOR VENTRAL MUSCULATURE (Plates XIX, XX, XXII).—The three lateral members of this series all take origin dorsally from the lumbo-dorsal fascia, which arises from the surface of the dorsal musculature and from the tips of the transverse processes of the lumbar vertebræ. Posteriorly, the fascia finds attachment to the anterior spine of the ilium. Below this, it passes over the surface of the "quadratus lumborum" (*pubo-ischio-femoralis internus, partim*), to which it is closely adherent, without the formation of a distinct ilio-pubic ligament; some of the fibers of the underlying muscle attach to the inner surface of the fascia.



## OBLIQUUS ABDOMINIS EXTERNUS

Obliquus descendens, Buttmann; obliquus externus abdominis, Gorski; obliquus externus, Stannius, Hair, and Maurer; and obliquus abdominis externus, Gadow.

The two portions of the muscle are not well separated in the lumbar region. The fibers arise from the lumbo-dorsal fascia and run postero-ventrally to insert (1) by a tendon which reaches the anterior edge of the acetabulum beneath the ambiens; (2) into the posterior dorsal end of the last abdominal rib, whence the origin is continued into a strong tendon which passes to the external edge of the pubis; (3) by an aponeurosis which lies over the main portion of the rectus but beneath the trunco-caudalis portion.

These relations correspond in general with the usual reptilian arrangement; the first-mentioned insertion appears to correspond with the usual insertion into the process lateralis pubis, the second with the insertion into the pubo-ischiadic ligament.

## OBLIQUUS ABDOMINIS INTERNUS

Obliquus internus, Buttmann, Stannius, and Hair; obliquus abdominis internus, Gadow; and intercostalis internus, abdominal part, Maurer.

The muscle arises dorsally from the fascia lumbo-dorsalis and runs ventro-anteriorly to insert into the posterior true ribs and the anterior abdominal ribs.

## TRANSVERSUS ABDOMINIS

Transversus abdominis, Buttmann and Gadow; transversalis, Hair; and transversus, Stannius and Maurer.

Arises from the deep surface of the lumbo-dorsal fascia and runs ventrally, inserting on the deep surface of the rectus.

## RECTUS ABDOMINIS

Rectus abdominis and pyramidalis, Buttmann, Stannius, Gorski, and Hair; and rectus abdominis, Gadow and Maurer.

The main portion of the rectus passes backwards as a strong muscular mass, with the abdominal ribs interrupting its external portion, while the internal portion is without interruption in the abdominal region. Both parts insert on to the last abdominal rib, none of the fibres attaching directly to the pelvis, such attachment being afforded only by the fact that this rib is attached to the pubis by membranous tissue ventrally and by a strong tendon laterally. Externally, the rectus is covered by the aponeurosis of the obliquus externus and by that special



portion of the muscle about to be described. Internally, it is in relation to the transversus.

In addition, there is a posterior portion of the rectus called trunco-caudalis by Maurer and considered by Gadow as a rectus lateralis and ventralis, *partim*. This arises in several layers from the surface of the principal portion of the rectus and the obliquus externus, from the posterior edge of the last abdominal rib, and from the anterior end of the membranous anterior continuation of the pubic surface. The deeper portion of these fibers inserts on to the posterior edge of the pubis, the more superficial portion passes on caudally over the ventral surface of ischio-caudalis, on to which it inserts.

As stated by Maurer, the rectus internus of Gadow is merely that portion of the rectus proper which is not interrupted by the abdominal ribs.

#### ILIO-ISCHIO-CAUDALIS

Plates XIX, XX, XXII, XXIII

No name, p. 13 (*partim*), Buttman; ischiococcygeus, Stannius, and Gorski; ilio-ischio-coccygeus, Hair; and ilio-ischio-caudalis, Gadow.

This muscle occupies the ventral half of the tail on either side, between the transverse processes and the mid-line ventrally. Anteriorly, it is split by the coccygeo-femoral muscles into two portions, one attaching to the posterior edge of the ilium at the level of the transverse processes, and the other inserting at the postero-external angle of the ischium. Near the pelvis are fibers which run nearly at a right angle to the general course of the muscle (transversus perinei). Ventrally, these fibers form two bundles, one inserting into the sphincter cloacæ, the other inserting on to the ischium. The anterior border of these muscles corresponds in position to the lacertilian ilio-ischiadic ligament; one head of the flexor tibialis internus arises from it.

#### EXTENSOR FEMORIS

Plates XIX to XXII

##### (a.) Ilio-tibialis

Rectus femoris, vastus externus and semi-membranosus, Buttman; "streck-muskelmasse," 1-2 heads + flexores abductores (*partim*), Stannius; sartorius, tensor fasciæ-latæ and glutæus maximus (*partim*), Gorski; gluteus maximus, tensor fasciæ femoris and biceps (*partim*), Hair; sartorius (in *Alligator*) or gluteus minimus (in *Crocodilus*), gluteus maximus, and agitator caudæ, Haughton; and extensor ilio-tibialis (two parts) and biceps (*partim*), Gadow.

The long iliac portion of the main extensor mass of the thigh. It arises by three heads, all tendinous, from the dorsal edge of the iliac



blade. The smallest head arises from the region near the anterior spine and, passing underneath the smaller portion of the ambiens, ends on the surface of the femoro-tibialis. The next posterior, the largest of the three, has a line of origin from a large part of the dorsal edge of the iliac blade, and blends with the tendon of the femoro-tibialis near the knee. The third and most posterior head arises behind and dorsal to the ilio-fibularis (in the sense used here) and proximal to the knee joins the common extensor tendon but also sends a tendon distally and externally to join that of the ambiens.

Gadow, following earlier writers, homologizes the third head with a portion of the ilio-fibularis (biceps). But it arises external (dorsal) to the true biceps muscle, almost in continuity with the main portion of ilio-tibialis and its insertion is definitely a part of that of the extensor mass. It seems obviously merely a portion of the ilio-tibialis, which has become separated from that muscle, as has the small anterior slip.

The muscle has a double (crural and sacral) innervation, the line of division passing through the middle head.

#### (b.) Ambiens

Vastus internus and gracilis, Buttmann; "streckmuskelmasse," 3+4 heads, Stannius; "oberflächliche strecher" and rectus femoris, Gorski; rectus femoris and sartorius, Hair; rectus femoris and tensor vaginae femoris (*Alligator*) or sartorius (*Crocodilus*), Haughton; and ambiens, Gadow.

This muscle consists of two quite distinct elements. The larger head arises at the junction, anteriorly, of the ilium and the pre-acetabular ramus of the ischium or the cartilage which precedes it. Near the knee, besides joining in part with the common extensor tendon, it forms a remarkable rounded tendon which passes through the extensor tendon, across the knee, to the external surface of the leg, where it joins the external head of the gastrocnemius. The small head arises from the base of the pubis and, passing laterally, unites with the ilio-tibialis just beyond the middle of the thigh.

#### (c.) Femoro-tibialis

Cruralis, Buttmann; cruræus and vasti, Stannius, Hair, and Haughton; cruralis and vasti, Gorski; and femoro-tibialis, Gadow.

This arises fleshily from the greater part of the shaft of the femur and inserts, together with the ilio-tibialis, into a tendon which reaches the head of the tibia. The internal head has much the same relations as the femoro-tibialis of lizards and *Sphenodon*, being bounded by the adductors antero-ventrally, the ilio-femoralis posteriorly (externally) and the



pubo-ischio femoralis internus proximally. In the Crocodilia, however, an additional external head is found, which passes between the ilio-femoralis and the adductors on the posterior (external) aspect of the bone.

#### ILIO-FIBULARIS

Semitendinous, Buttmann; flexores abductores (*partim*), Stannius; glutæus maximums (*partim*, *p*) Gorski; biceps (*partim*), Haughton; biceps, Hair; and ilio-fibularis (*partim*), Gadow.

This muscle arises from the external surface of the ilium, slightly ventral to the ilio-tibialis and appearing at its origin between the main and posterior heads of that muscle. It inserts into the head of the fibula and is connected with the external head of the gastrocnemius as well.

Previous writers also homologize the posterior head of ilio-tibialis with this muscle. This question has been discussed above.

#### PUBO-ISCHIO-FEMORALIS INTERNUS

##### Plates XIX to XXII

Psoas major and iliacus internus, Buttmann and Gorski; abductor femoris + iliacus internus, Stannius; psoas magnus and iliacus, Haughton; adductor femoris (psoas) and iliacus, Hair; and quadratus lumborum and pubo-ischio-femoralis internus, part III, Gadow.

This muscle is in two parts. One (Gadow's "quadratus lumborum") arises from the bodies and under surfaces of the transverse processes of the six lumbar vertebræ and passes backward to insert by a broad tendon on the dorsal surface of the proximal portion of the femur; the tendon is partially interrupted by the proximal part of the area of origin of the femoro-tibialis internus. The second and more ventral part arises from the internal surface of the ilium and ischium dorsally and the ventral portions of the sacral ribs, and runs out anteriorly beneath the preceding part to insert fleshily on to the femur antero-ventrally to the area of insertion of the more dorsal portion. The innervation of both parts is crural.

Gadow homologizes the dorsal portion, apparently because of its lumbar origin, with the quadratus lumborum, an axial muscle. Its insertion is proximal to that of the femoro-tibialis on the dorsal surface of the femur and corresponds to that of one of the two portions of the more typical pubo-ischio-femoralis internus (Romer, 1923). It appears to be that muscle mass, the origin of which has moved dorsally and anteriorly in correlation with the changed type of locomotion found in the Archosauria.



The remaining portion of the pubo-ischio-femoralis internus, as defined in this paper, is Gadow's part III. His parts I and II are considered under pubo-ischio-femoralis externus.

The insertion of the ventral portion of the pubo-ischio-femoralis internus is that of the more anterior part of the pubo-ischio-femoralis internus of lizards and *Sphenodon*, that is, antero-ventral to femoro-tibialis, antero-dorsal and proximal to the adductor(s), dorsal to the coccygeo-femorales, and antero-distal to the insertion of the other portion of the same muscle. The shifting posteriorly of the insertion of pubo-ischio-femoralis externus on the ventral surface gives the only difference in the relations of the insertion.

### ILIO-FEMORALIS

Plates XIX to XXII

Quadratus femoris, Buttmann; glutæus medius, Gorski, Haughton, and Hair; glutæus, Stannius; obturateur externe, chef iliaque, Sabatier; and caudi-ilio-femoralis, Gadow.

The ilio-femoralis arises from a large expanse of the ilium above and behind the acetabulum, beneath the ilio-tibialis and anterior to the coccygeo-femoralis brevis and ilio-fibularis. It inserts on to the external (posterior) edge of the femur, between internal and external heads of the femoro-tibialis for the greater part of the length of the shaft. Its innervation is characteristically double, crural and sacral.

It is closely comparable with the typical reptilian ilio-femoralis, differing only in the fact that the presence of the external head of femoro-tibialis in the Crocodilia has changed its posterior relations at its insertion. Gadow calls it "caudi-ilio-femoralis" (coccygeo-femoralis brevis); but it is quite distinct from that muscle, which Gadow includes under coccygo-femoralis longus ("caudi-femoralis").

### ISCHIO-TROCHANTERICUS

Plates XX to XXII

Pectinæi inferiores (*partim*), Buttmann; gemellus, Stannius and Hair; *h*, part of "auswärtsroller des Oberschenkels," Gorski; and obturator externus (*Alligator*) or quadratus femoris (*Crocodylus*), Haughton; and pubo-ischio-femoralis posterior (*partim*), Gadow.

A small muscle arising from the posterior portion of the inner surface of the ischium and running up and out to insert tendinously at the outer dorsal edge of the femur near the head. An ischiatic innervation. It is comparable to the typical reptilian muscle. Gadow homologizes it correctly but includes with it the posterior adductor, which arises from the outer surface of the ischium in the same region.



LONG FLEXORS TO LOWER LEG: PUBO-ISCHIO-TIBIALIS, FLEXOR  
TIBIALIS INTERNUS, FLEXOR TIBIALIS EXTERNUS

Plates XIX, XXII, XXIII

Triceps flexor cruris and sartorius, Buttmann; "flexores des unterschenkels" (two groups), Stannius; gracilis, semimembranosus, semitendinosus, Gorski and Hair; gracilis, semimembranosus, third or long adductor, extensor femoris caudali accessorius (Crocodile) or Nos. 18 and 22 (Alligator), Haughton; and flexor tibialis internus, flexor tibialis externus, Gadow.

This group, in the alligator, consists of six muscles which unite at their insertion into two groups of three each. We shall consider these groups in turn and then discuss their homologies.

EXTERNAL GROUP.—This has three heads as follows.

(1.) A slip arising from the anterior edge of the main blade of the ischium just below the acetabulum. It passes laterally anterior to pubo-ischio-femoralis externus III but posterior to adductor I and joins the other two components proximal to the knee.

(2.) A small slip which arises from the external ventral posterior portion of the ischiadic blade, near the insertion of ischio-caudalis, and unites with the third part half-way to knee.

(3.) A large belly from the posterior angle of the iliac blade just ventral to the flexor tibialis externus. It passes out and ventrally unites with 2 and then with 1. The common tendon passes to the internal side of the knee to insert into the tibia internal to all the lower leg flexors. The first two are innervated by the obturator nerve, the third is innervated by the ischiadic plexus.

These three muscles are all considered by Gadow as constituting part of the flexor tibialis internus (Theil I, 1, 2, and 3). But if we compare with the lacertilian condition, we find there an outer group of flexors, usually arising in three parts and inserting close together on the internal (anterior) side of the tibia, medial to all the flexor mass of the lower leg (the third member of the group tends to insert more proximally) (Romer, 1922, p. 570). These muscles include the pubo-ischio-tibialis and two portions of the flexor tibialis internus. The two portions of the flexor tibialis internus associated with this group arise from the posterior portion of the ischium near the tubercle and from the ligamentum ilio-ischiadicum. This agrees well with the two more posterior portions of the crocodilian triad, except that the third member of the latter (Gadow's I, 3) arises from the ilium at the upper end of the ligament instead of the ligament itself. But the anterior part, instead of arising as does the pubo-ischio-tibialis of the lizard from the whole ventral expanse of the girdle, is confined, in the Crocodilia, to a narrow area at the anterior edge



of the ischium. This muscle (Gadow's I, 1) is then in all probability the pubo-ischio-tibialis, which, owing to the great change in the pubo-ischiadic plate, has had its area of origin greatly diminished.

Gadow, although finally deciding that the pubo-ischio-tibialis was not represented in the Crocodilia, suggests in a footnote (p. 404) that two parts of his "Theil I, 1 and 2" might be homologized with pubo-ischio-tibialis. The innervations do not stand in the way of the suggested homologies; both pubo-ischio-tibialis and flexor tibialis internus in the Lacertilia have a double (obturator and ischiadic) innervation.

We may reasonably conclude then that the superficial medially inserting triad of flexors in the Crocodilia is composed of a reduced pubo-ischio-tibialis and two heads of flexor tibialis internus.

INTERNAL GROUP.—This likewise consists of three muscles, Gadow's flexor tibialis internus II and III and his flexor tibialis externus. As Gadow has shown (1882, fig. 50), they have a common insertion by a double tendon, of which one part reaches the tibia between the two heads of the gastrocnemius and the other runs along the external head of that muscle, with which it unites near the foot.

The most ventral and anterior of the three heads (Gadow's flexor tibialis internus III) arises from the posterior margin of the ischium behind the posterior portion of the adductor and proximal to the area of origin of that muscle. The next (Gadow's flexor tibialis internus II) arises from the fascia at the anterior edge of the ilio-ischio-caudalis from the position of the lacertilian ilio-ischiadic ligament. The third, a large head (flexor tibialis externus) arises tendinously from the posterior end of the dorsal edge of the iliac blade, just above the iliac head of flexor tibialis internus.

The iliac portion is certainly the lacertilian flexor tibialis externus, the latter, however, usually arising a bit more ventrally from the ilio-ischiadic ligament. The two remaining heads may be homologized, although perhaps not exactly, with the usual single belly of flexor tibialis internus associated with the deep flexors in lizards and *Sphenodon*. The lacertilian head arises from the ilio-ischiadic ligament in the position of one of the two heads under consideration; the other crocodilian head arises from the ischium, ventral to the position of the usual lacertilian head.

The innervations of this group are sacral in character. This and the fact that all the origins are posteriorly placed, precludes any attempt to homologize one of these heads with the lizard or *Sphenodon* pubo-tibialis, which has an anterior origin and apparently an obturator innervation.



The pubo-tibialis, which forms one of the deep triad in more typical reptiles, has been lost in the Crocodilia.

The chief differences between the long flexors of the lizards and the Crocodilia are that in the latter the pubo-tibialis has been lost, the pubo-ischio-tibialis reduced, and with the loss of the ilio-ischiadic ligament the flexors originating from it have removed their origins to the adjacent bones (except for one small slip).

#### ADDUCTOR FEMORIS

Plates XIX, XXII, XXIII

Adductores, Buttman; adductores, primus + secundus, Stannius and Hair; adductores, longus + magnus, Gorski; adductores, brevis + magnus (Alligator), first + second (Crocodile), Haughton; and ischio-femoralis + pubo-ischio-femoralis posterior (*partim*), Gadow.

This consists of two parts, both arising from the outer side of the ischium but separated by part III of pubo-ischio-femoralis externus. The two converge to a long and narrow area of insertion on the ventral side of the femur, comparable to that of typical reptiles, except that the presence of an external head of femoro-tibialis separates it from the ilio-femoralis. The double (obturator and sacral) innervation of the lacertilian muscle is repeated in the more posterior of the two heads.

Gadow correctly homologizes the anterior head with the "ischio-femoralis" (adductor) of other reptiles, but he includes the posterior head with the ischio-trochantericus, calling the two muscles pubo-ischio-femoralis posterior.

The division into two parts and the fleshy origins are in marked contrast to the usual reptilian condition.

#### PUBO-ISCHIO-FEMORALIS EXTERNUS

Plates XIX, XXIII

Pectinei superiores et inferiores (*partim*), Buttman; obturator internus + obturator externus + quadratus femoris, Stannius and Hair; pectinei + adductor brevis, Gorski; pectineus + marsupiales, Haughton; obturateur externe, chef pubien + chef ischiatique + pectiné ou pubien interne, Sabatier; and pubo-ischio-femoralis externus + pubo-ischio-femoralis internus, I + II, Gadow.

This consists of three main portions arising (1) from the dorsal (internal) surface of the pubis and the adjacent edge of the last abdominal rib; (2) from the external (ventral) surface of the pubis and the membrane between it and the last abdominal rib; (3) from the outer surface of the ischium between the two heads of the adductor femoris. With the first two are associated shorter and smaller heads arising beneath them



from the proximal portion of either surface of the pubis. With the third is associated a small head separated from it at its origin by the anterior head of the adductor femoris and the pubo-ischio-tibialis.

All these portions unite in a tendinous insertion at the posterior ventral edge of the femur close to the head.

This disposition is in marked contrast to the pubo-ischio-femoralis externus of lizards and *Sphenodon*. Part I, as here described, arises from the dorsal or internal surface of the pubis; and consequently Gadow homologizes it with part of pubo-ischio-femoralis internus, although its obturator innervation and its insertion show that this is impossible. Further, the usual origin of the muscle from the outer surface is in one solid mass, as contrasted with two widely separated surfaces in the Crocodilia.

#### COCCYGEO-FEMORALIS BREVIS

##### Plates XIX, XXIII

Obturator-internus, Buttmann; pyriformis, Stannius; "auswärtsroller des ober-schenkels" (*partim*), Gorski; quadratus femoris (Alligator), obturator externus (Crocodile), Haughton; pyriformis + glutæus minimus, Hair; and caudi-femoralis (*partim*), Gadow.

This muscle arises from the last sacral and first caudal vertebræ and passes outward beneath the posterior end of the ilium. Here it receives another slip from the posterior edge of that bone and then inserts on to the femur dorsal to the insertion of the coccygeo-femoralis longus.

Gadow calls this muscle caudi-ilio-femoralis in other reptiles but applies this name to the ilio-femoralis of the Crocodilia, where the coccygeo-femoralis brevis is considered as part of the following muscle.

#### COCCYGEO-FEMORALIS LONGUS

Pyriformis, Buttmann; subcaudalis, Stannius; "femoro-péroneo-coccygien Cuv.," Gorski; extensor femoris caudalis, Haughton; femoro-perineo-coccygius, Hair; and caudi-femoralis (*partim*), Gadow.

This arises from the bodies and lower sides of the transverse processes of the caudal vertebræ, approximately the third to the fifteenth. It runs forward, constantly increasing in size and covered by the ilio-ischio-caudalis, to end in a thick tendon which inserts into the "fourth trochanter" of the femur. From the side of this tendon another extends, deeply placed at right angle to the knee region, where it inserts ventrally into the fibula. This is similar to the lacertilian muscle.

As noted above, Gadow includes coccygeo-femoralis brevis with this muscle.



TABLE OF SYNONYMY  
Gadow (1882) and The Present Paper

| GADOW, 1882                                                                                                                                                                                       | ROMER, 1923                                                                                                                                                                                      |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Axial Muscles                                                                                                                                                                                     |                                                                                                                                                                                                  |
| “Rückenmuskeln”<br>Obliquus abdominis externus.<br>Obliquus abdominis internus<br>Transversus abdominis<br>Rectus abdominis<br>Ilio-ischio-caudalis                                               | Dorsalis trunci, Dorsalis caudæ<br>Obliquus abdominis externus<br>Obliquus abdominis internus<br>Transversus abdominis<br>Rectus abdominis<br>Ilio-ischio-caudalis                               |
| Dorsal Group                                                                                                                                                                                      |                                                                                                                                                                                                  |
| Extensor ilio-tibialis, Part II<br>Extensor ilio-tibialis, Part I<br>Ilio-fibularis, Part II<br>Ambiens, Part I<br>Ambiens, Part II<br>Femoro-tibialis, inner head<br>Femoro-tibialis, outer head | Ilio-tibialis, Part I<br>Ilio-tibialis, Part II<br>Ilio-tibialis, Part III<br>Ambiens, Part I<br>Ambiens, Part II<br>Femoro-tibialis internus<br>Femoro-tibialis externus                        |
| Ilio fibularis, Part I                                                                                                                                                                            | Ilio-fibularis                                                                                                                                                                                   |
| Pubo-ischio-femoralis internus, Part III<br>Quadratus lumborum<br>Caudi-ilio-femoralis<br>Pubo-ischio-femoralis posterior ( <i>partim</i> )                                                       | Pubo-ischio-femoralis internus, Part I<br>Pubo-ischio-femoralis internus, Part II<br>Ilio-femoralis<br>Ischio-trochantericus                                                                     |
| Ventral Group                                                                                                                                                                                     |                                                                                                                                                                                                  |
| Flexor tibialis internus I, 1<br>Flexor tibialis internus I, 2<br>Flexor tibialis internus I, 3<br>Flexor tibialis internus, III<br>Flexor tibialis internus, II<br>Flexor tibialis externus      | Pubo-ischio-tibialis<br>Flexor tibialis internus Part I<br>Flexor tibialis internus Part II<br>Flexor tibialis internus Part III<br>Flexor tibialis internus Part IV<br>Flexor tibialis externus |
| Pubo-ischio-femoralis<br>Pubo-ischio-femoralis posterior ( <i>partim</i> )                                                                                                                        | Adductor femoris, Part I<br>Adductor femoris, Part II                                                                                                                                            |
| Pubo-ischio-femoralis internus, Parts I and II<br>Pubo-ischio-femoralis externus, Part I<br>Pubo-ischio-femoralis externus, Part II                                                               | Pubo-ischio-femoralis externus, Part I<br>Pubo-ischio-femoralis externus, Part II<br>Pubo-ischio-femoralis externus, Part III                                                                    |
| Coccygeo-femoral Muscles                                                                                                                                                                          |                                                                                                                                                                                                  |
| Caudi-femoralis, Part I<br>Caudi-femoralis, Part II                                                                                                                                               | Coccygeo-femoralis longus<br>Coccygeo-femoralis brevis                                                                                                                                           |



## COMPARISON OF AVIAN AND REPTILIAN PELVIC MUSCLES

Following the name of each reptilian muscle its probable avian homologues are discussed. For the purposes of this paper the nomenclature of Gadow and Selenka in Bronn's 'Thierreich' (1891) has been adopted for bird muscles and the reader is referred to that volume for detailed descriptions and for illustrations.

## AXIAL MUSCLES

The dorsal (spinal) muscle mass is completely interrupted by the sacrum, as contrasted with the reptilian condition. This has separated off the caudal portion as the levator coccygeus, connecting the posterior end of the ilium with the remaining caudal vertebræ.

The abdominal muscles are the same, although the modifications in the pelvic girdle have necessarily modified their attachments. The obliquus externus inserts on to the whole anterior edge of the pubis. The origin of the obliquus internus usually is from the preacetabular portion of the ilium, then bridging over the gap below, to the middle portion of the anterior edge of the pubis. The origin of the transversus likewise bridges over the gap between the preacetabular portion of the ilium and the anterior edge of the pubis. The rectus inserts on to the distal halves of the pubes. The differences in the pelvic relations are clearly associated with the forward growth of the ilium and the backward turning of the pubis. It will be noted that the iliac attachments are ventral to the whole group of anterior muscles running from the ilium to the femur. The reptilian obliqui and transversus form a bridge posteriorly over the region of exit of pubo-ischio-femoralis internus from the internal aspect of the girdle. Since this muscle now arises from the ilium, the need for such an interruption in the attachments of the lateral muscles has been done away with.

The ilio-coccygeus from the ilium to the tail and the depressor caudæ from the last sacral vertebra along the ventral side of the transverse processes of the tail vertebræ, represent a reduced ilio-caudalis. The pubo-coccygei represent the ischio-caudalis. The more internal of the two, from its position between the obturator and the transversus, appears to represent the deep portion of the ventral caudal musculature, which is generally reduced in the Reptilia. The transverso-analis represents the transversus perineus of reptiles in a somewhat variable fashion.

## TRICEPS

We may consider in order (a) ilio-tiabilis, (b) ambiens, and (c) femoro-tibialis.



ILIO-TIBIALIS.—As homologues of this muscle may be considered the ilio-tibialis internus s. “sartorius” and ilio-tibialis, the latter usually divided into anterior, median and posterior parts. They are dorsal in origin and gain insertion into the tibia either directly or through the intervention of the patella or the patellar ligament, with the femoro-tibialis. The “sartorius” and anterior portion of the ilio-tibialis proper are innervated from the crural plexus, the posterior portion from the sacral plexus. This double innervation is similar to that of reptiles. The ilio-tibialis is often two-headed in the lizards; the triple ilio-tibialis of the Crocodilia is, however, closer to the bird condition. That the “sartorius” is essentially part of this group is indicated by the fact that it is often more or less fused with the ilio-tibialis anterior. The origins are similar in character to the reptilian, in general from the dorsal border of the ilium, mostly tendinously posteriorly, and more fleshily in the case of the “sartorius.”

The “sartorius” is not, of course, the mammalian muscle of that name (which is the sauropsid ambiens) nor can it equal the reptilian pubo-tibialis, which is a ventral muscle (Romer, 1922, p. 563).

AMBIENS.—This muscle, running from the region of the pubic spine and terminating in a tendon which crosses the knee joint to the outer side to end in relation with the lower leg musculature, is indisputably the muscle of the same name in reptiles and resembles strikingly the main portion of the alligator ambiens. It leaves the girdle ventral to the pubo-ischio-femoralis internus as in reptiles. There is, in general, no representative of the smaller portion of the crocodilian ambiens. In many higher birds the muscle is lost or seen reduced, and showing a probable secondary return to the original condition in a closer union with the main elements of the ilio-tibialis.

FEMORO-TIBIALIS.—The femoro-tibialis is in two main portions, which seem to be essentially similar to the internal and external portions of the same muscle in Crocodilia. But because the ilio-femoralis is restricted to the proximal part of the femur, the division into two portions is not so clear; further, the great growth of the muscle, with a subdivision into numerous heads and a tendency to push the area of insertion towards the acetabulum wherever possible, makes the homologues of the smaller subdivisions difficult and unprofitable.

#### ILIO-FIBULARIS

It arises from the dorsal edge of the postacetabular ilium, usually covered by the ilio-tibialis, and running through a peculiar “tendon sling” attached to the femur and the external head of the gastrocnemius, inserts



on to the fibula. The area of origin postero-dorsally and its position slightly deeper than the ilio-tibialis are reminiscent of the Reptilia. The insertion internal to a portion of the gastrocnemius is in contrast to the usual reptilian condition; but in the Crocodilia it is in intimate relation with the outer (femoral) head of the gastrocnemius; out of this connection may have arisen its changed insertion and the new tendon arrangement, which is connected with the external head of the gastrocnemius. Gadow notes that in *Struthio* the ilio-fibularis has a tendinous connection with gastrocnemius.

#### PUBO-ISCHIO-FEMORALIS INTERNUS

We have noted that in the Crocodilia this muscle is entirely antero-dorsal in origin as contrasted with the primitive reptilian condition. I purpose to homologize with this muscle the bird muscles with an origin in a similar region; although this region, instead of being a bare expanse along the lumbar vertebræ, is now covered by an anterior extension of the ilium (Romer, 1923). These muscles include the ilio-trochanterici and ilio-femoralis internus. The insertion of these muscles is in general divisible into two regions, one more postero-dorsal, comparable to the "quadratus lumborus" insertion, and another more anterior and ventral, corresponding to the "p. i. f. i. Part III" insertion.

Gadow (1880) at first reached the same conclusion, but later (1891) modified his views, stating that of this group only the ilio-femoralis internus belonged to the pubo-ischio-femoralis internus (quadratus lumborum) and that the ilio-trochanterici are derived from the ilio-femoralis (together with the ilio-femoralis externus). The only reason advanced for this conclusion is that in a few cases the ilio-trochanterici have a slight innervation from the sacral plexus, which is not typically the case with pubo-ischio-femoralis internus; a double innervation from both crural and sacral plexes is typical of the ilio-femoralis. But, as he notes, this innervation is infrequent and of slight extent; the division between the two plexi is often through the ilio-femoralis externus, giving that muscle in itself the characteristics of the reptilian ilio-femoralis. Further, it seems probable that ilio-femoralis and pubo-ischio-femoralis internus are differentiations from a primitively single muscle mass (Romer, 1922, p. 565), with a double innervation; it is not improbable that in the ancestors of the birds the separation between the two muscles corresponded very nearly to the division between the two plexes, and that slight variations would cause the sacral innervation to cross the division into the pubo-ischio-femoralis internus or the contrary (as in most reptiles).



## ILIO-FEMORALIS

It is agreed that the avian ilio-femoralis externus is derived from the reptilian ilio-femoralis and, if the above reasoning holds, it is the only muscle so derived. It has an innervation which is often purely sacral but sometimes crural as well, the latter more closely resembling the typical reptilian condition. It runs rather straight out from the ilium to the postero-external region of the femur, contrasting with the more antero-posterior course of the ilio-trochanterici. But its insertion does not extend so far down the femur and hence it does not differentiate internal and external heads of the femoro-tibialis so markedly as its reptilian predecessor. It is smaller than the reptilian muscle but like it arises from a surface above the acetabulum, covered by the ilio-tibialis.

## ISCHIO-TROCHANTERICUS

There seems no doubt that this muscle has given rise to the ischio-femoralis of the birds. This is a deep muscle, inserting, as in reptiles, near the head of the femur and arising posteriorly in the region of the ischium. In Reptilia the origin is from the inner surface of the ischium but the great change this bone has undergone in the evolution of the birds has caused its origin to be from the outer surface and often on to the membrane covering the area between ischium and pubis.

## LONG FLEXORS: PUBO-TIBIALIS, PUBO-ISCHIO-TIBIALIS, FLEXOR TIBIALIS INTERNUS, AND FLEXOR TIBIALIS EXTERNUS

There has been great reduction in this group; there are usually but two muscles which can be assigned to it, as contrasted with the half-dozen or so common among reptiles.

The more posterior and dorsal of the two is the caud-ilio-flexorius, which arises from the dorsal edge of the posterior portion of the ilium and from the anterior caudal vertebræ, and inserts (1) by an accessory muscle into the distal part of the shaft of the femur; (2) into the tibia and internal head of the gastrocnemius. Gadow seems correct in homologizing this with the flexor tibialis externus of reptiles; there are, however, points of difference. An iliac origin for this muscle is found in the Crocodilia at least, and through the ilio-ischiadic ligament in many lizards; the caudal extension of the origin is probably secondary, although *Sphenodon* furnishes a parallel.

The insertion into tibia and gastrocnemius is typically reptilian. The "accessory" muscle, which binds it to the femur, is very peculiar. Gadow suggests that this is a partial retention of a primitive insertion



running the whole way from trochanters to tibia; but there is no indication of such a muscle in any reptile. It seems more probable that, as certain of his figures suggest, the muscle is a slip separated from the gastrocnemius (Gadow, 1891, Plate XIII *b*, figs. 2, 5, 6). It would thus be, as Gadow admits it appears to be, an origin rather than an insertion.

The other avian member of this group is the ischio-flexorius. This arises usually from the ischium and sometimes to a slight extent from the pubis, and inserts into the tibia between the heads of the gastrocnemius.

Gadow seems correct in homologizing it with some portion of the flexor tibialis internus. It has an ischiadic innervation, which makes a homology with the pubo-tibialis or anterior part of pubo-ischio-tibialis impossible. Its area of insertion is in contrast with pubo-ischio-tibialis and the more external portions of flexor tibialis internus and in agreement with the deeper portion or portions of the latter muscle. This is strengthened by its frequent association with the caud-ilio-flexorius and gastrocnemius, paralleling the association of the deep part of flexor tibialis internus with flexor tibialis externus and gastrocnemius in reptiles. Its closest homologue in reptiles would be some such slip as the third portion of flexor tibialis internus in the Crocodilia.

#### ADDUCTOR FEMORIS

This is represented by the pubo-ischio-femoralis. This arises from the pubo-ischium by two heads, which insert close to one another on a line extending most of the length of the femur to the internal condyles.

The Crocodilia have also two parallel heads, although the more antero-ventral one does not, as in birds, extend on to the pubis as well as the ischium. The avian muscles have an obturator innervation; the obturator innervates the anterior and part of the posterior adductor of the Crocodilia.

Gadow would homologize this muscle with part of pubo-ischio-femoralis externus; but the insertion is in marked contrast with that of the reptilian muscle mentioned, and in perfect agreement with that of the adductor.

#### PUBO-ISCHIO-FEMORALIS EXTERNUS

The obturator and accessory obturator muscles represent this muscle, in part at least, in birds, as Gadow states. Their proximal insertion and obturator innervation agree with this. Apparently in correlation with the backwardly directed position of the pubis, the muscle is no



TABLE OF MUSCULAR HOMOLOGIES BETWEEN TYPICAL REPTILES,  
CROCODYLIANS, AND BIRDS

| TYPICAL REPTILES                                                                  | CROCODYLIA                                                                                                      | BIRDS                                                                                                               |
|-----------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------|
| Dorsalis trunci including<br>longissimus dorsi, ilio-<br>costalis, dorsalis caudæ | The Same                                                                                                        | Dorso-spinal muscles, in-<br>cluding longissimus dorsi,<br>ilio-costalis, levator coc-<br>cygeus.                   |
| Obliquus abdominis<br>externus                                                    | Obliquus abdominis<br>externus                                                                                  | Obliquus abdominis<br>externus                                                                                      |
| Obliquus abdominis<br>internus                                                    | Obliquus abdominis<br>internus                                                                                  | Obliquus abdominis<br>internus                                                                                      |
| Transversus abdominis                                                             | Transversus abdominis                                                                                           | Transversus abdominis                                                                                               |
| Rectus abdominis                                                                  | Rectus abdominis                                                                                                | Rectus abdominis                                                                                                    |
| Ilio-caudalis                                                                     | Ilio-caudalis                                                                                                   | Ilio-coccygeus and depres-<br>sor coccygeus                                                                         |
| +                                                                                 | +                                                                                                               | +                                                                                                                   |
| Ischio-caudalis                                                                   | Ischio-caudalis                                                                                                 | Pubi-coccygeus                                                                                                      |
| Ilio-tibialis<br>(one or two parts),<br><i>crur</i> + <i>sac</i>                  | Ilio-tibialis I, <i>crur</i><br><br>Ilio-tibialis II, <i>crur</i> + <i>sac</i><br>Ilio tibialis III, <i>sac</i> | Ilio-tibialis internus<br>("sartorius," <i>crur</i> )<br>Ilio-tibialis (often 3 heads),<br><i>crur</i> + <i>sac</i> |
| Ambiens, <i>crur</i> .                                                            | Ambiens I, <i>crur</i><br>Ambiens II, <i>crur</i>                                                               | Ambiens, <i>crur</i>                                                                                                |
| Femoro-tibialis, <i>crur</i>                                                      | Femoro-tibialis internus,<br><i>crur</i><br>Femoro-tibialis externus,<br><i>crur</i>                            | Femoro-tibialis (several<br>divisions); <i>crur</i>                                                                 |
| Ilio-fibularis, <i>sac</i>                                                        | Ilio-fibularis, <i>sac</i>                                                                                      | Ilio-fibularis, <i>sac</i>                                                                                          |
| Pubo-ischio-femoralis<br>internus, <i>crur</i>                                    | Pubo-ischio-femoralis<br>internus I, <i>crur</i><br>Pubo-ischio-femoralis<br>internus II, <i>crur</i>           | Ilio-trochanterici<br>+<br>Ilio-femoralis internus,<br><i>crur</i> (+ <i>sac</i> )                                  |
| Ilio-femoralis, <i>crur</i> + <i>sac</i>                                          | Ilio-femoralis, <i>crur</i> + <i>sac</i>                                                                        | Ilio-femoralis externus, <i>sac</i><br>(+ <i>crur</i> )                                                             |
| Ischio-trochantericus, <i>sac</i>                                                 | Ischio-trochantericus, <i>sac</i>                                                                               | Ischio-femoralis, <i>sac</i>                                                                                        |
| Pubo-tibialis, <i>obt</i>                                                         | .....                                                                                                           | .....                                                                                                               |
| Pubo-ischio-tibialis,<br><i>obt</i> + <i>sac</i>                                  | Pubo-ischio-tibialis (re-<br>duced), <i>obt</i>                                                                 | .....                                                                                                               |
| Flexor tibialis internus,<br><i>obt</i> + <i>sac</i>                              | Flexor tibialis internus (4<br>parts), <i>obt</i> + <i>sac</i>                                                  | Ischio-flexorius (deep),<br><i>sac</i>                                                                              |
| Flexor tibialis externus,<br><i>sac</i>                                           | Flexor tibialis externus,<br><i>sac</i>                                                                         | Caud-ilio-flexorius, <i>sac</i>                                                                                     |
| Adductor femoris, <i>obt</i> + <i>sac</i>                                         | Adductor femoris (2 parts),<br><i>obt</i> + <i>sac</i>                                                          | Pubo-ischio-femoralis (2<br>parts), <i>obt</i>                                                                      |
| Pubo-ischio-femoralis<br>externus, <i>obt</i> + <i>sac</i>                        | Pubo-ischio-femoralis<br>externus (3 main parts),<br><i>obt</i>                                                 | Obturator + accessory<br>obturators, <i>obt</i>                                                                     |
| Coccygeo-femoralis longus<br>+                                                    | Coccygeo-femoralis longus<br>+                                                                                  | Caud-ilio-femoralis                                                                                                 |
| Coccygeo-femoralis brevis                                                         | Coccygeo-femoralis brevis                                                                                       |                                                                                                                     |



longer found on the outer surface of the pubis and ischium, but on the inner surface, where the apposition of the two bones has imprisoned it. Near the proximal foramen, where it escapes to the exterior, are found variable small accessory muscles.

#### COCYGEO-FEMORALIS

Caud-ilio-femoralis in birds. Its areas of origin are exceedingly variable but generally include one from the tail vertebræ and one from the ilium below the ilio-fibularis. The former is the primitive area of origin of the two reptilian muscles; in the Crocodilia the coccygeo-femoralis brevis has a slight area of origin from the external surface of the ilium, of which the bird iliac origin seems an expansion. The femoral insertion is not such a definite one as is usual in reptiles, nor is there the typical reptilian tendon from the longer of the muscles to the knee region; possibly the association of the muscle with the "accessory semi-tendinosus" of *Rhea* and *Dromæus* may be reminiscent of this.

#### DISTINCTIVE FEATURES OF ARCHOSAURIAN PELVIC MUSCULATURE

From the features which the Crocodilia and birds possess in common, in contrast to the more typical Reptilia, we may deduce a number of features which were probably possessed by the common archosaurian stock.

1.—There was a general tendency for a fragmentation of muscles, both living groups possessing at least half a dozen additional heads not separated out in typical reptiles. This is apparently associated with a greater diversity of limb movements.

2.—The ilio-tibialis, primitively in one, or at the most two, heads, split into three in the Crocodilia and usually into four in birds.

3.—The ambiens tendon crossing the knee was developed.

4.—The femoro-tibialis acquired an additional external head.

5.—The pubo-ischio-femoralis internus moved dorsally at its origin.

6.—The long flexors tended to become concentrated posteriorly, with the reduction (Crocodilia) or loss (birds) of pubo-ischio-tibialis, and the loss in both of pubo-tibialis.

7.—The adductor femoris divided into two portions.

8.—The caudi-femoralis brevis acquired an iliac head.

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## TABLE OF ABBREVIATIONS

## Plates XIX to XXV

|                         |                                           |
|-------------------------|-------------------------------------------|
| ad. 1, 2                | adductor femoris, parts 1 and 2           |
| amb. 1, 2               | ambiens, parts 1 and 2                    |
| c. f. b.                | coccygeo-femoralis brevis                 |
| c. f. l                 | " " longus                                |
| fem. tib. ext.          | femoro-tibialis externus                  |
| fem. tib. int.          | " " internus                              |
| fl. tb. ext.            | flexor tibialis externus                  |
| fl. tb. int. 1, 2, 3, 4 | " " internus, parts 1-4                   |
| il. fem.                | ilio-femoralis                            |
| il. fib.                | ilio-fibularis                            |
| il. is. c.              | ilio-ischio-caudalis                      |
| il. tib. 1, 2, 3        | ilio-tibialis, parts 1-3                  |
| is. tr.                 | ischio-trochantericus                     |
| o. a. e.                | obliquus abdominis externus               |
| o. a. i.                | " " internus                              |
| p. i. f. e 1, 2, 3      | pubo-ischio-femoralis externus parts 1-3  |
| p. i. f. i 1, 2         | pubo-ischio-femoralis internus parts 1, 2 |
| p. i. t.                | pubo-ischio-tibialis                      |
| r. abd.                 | rectus abdominis                          |
| tr. abd.                | transversus abdominis                     |
| tr. per.                | transversus perinei                       |



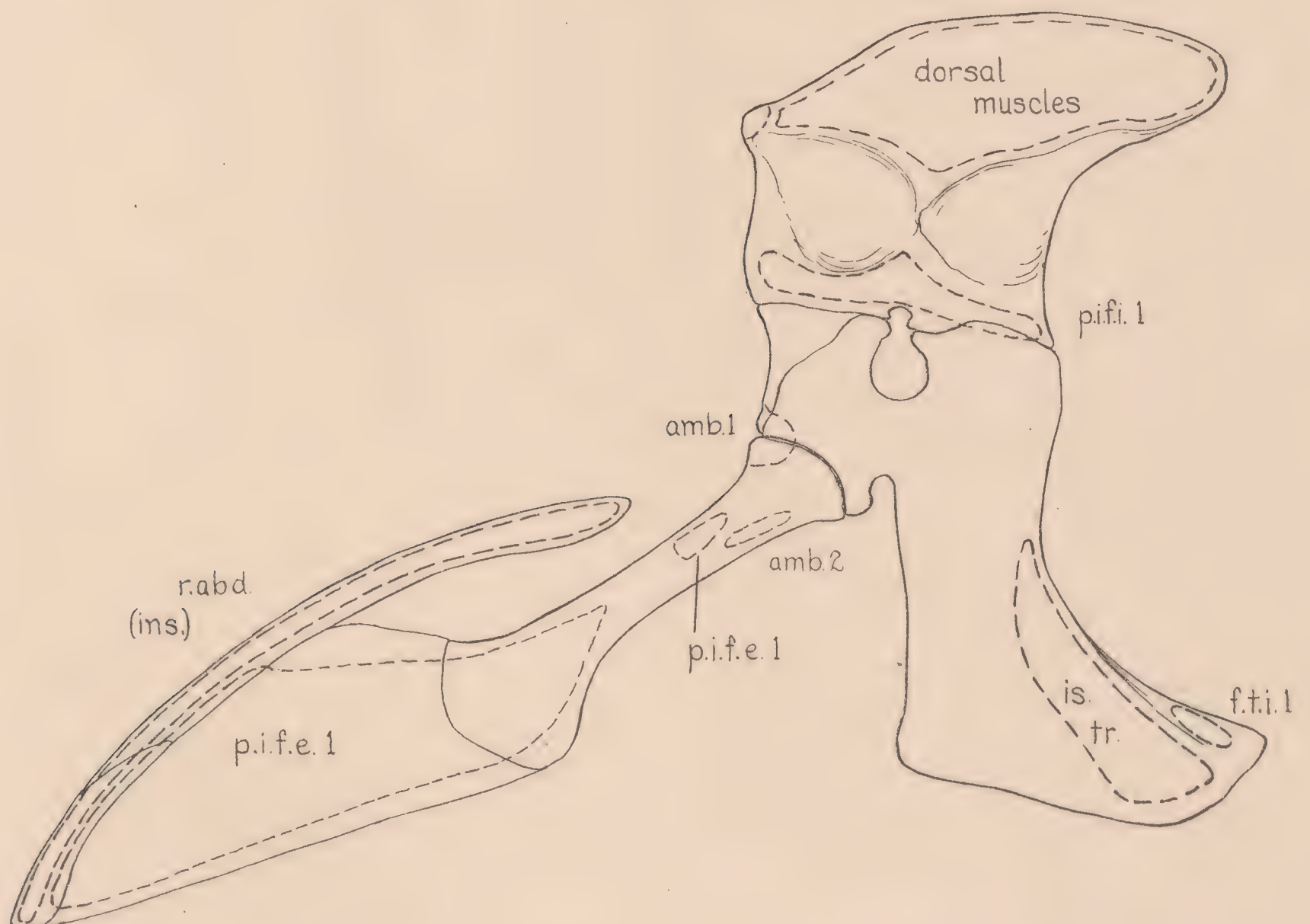
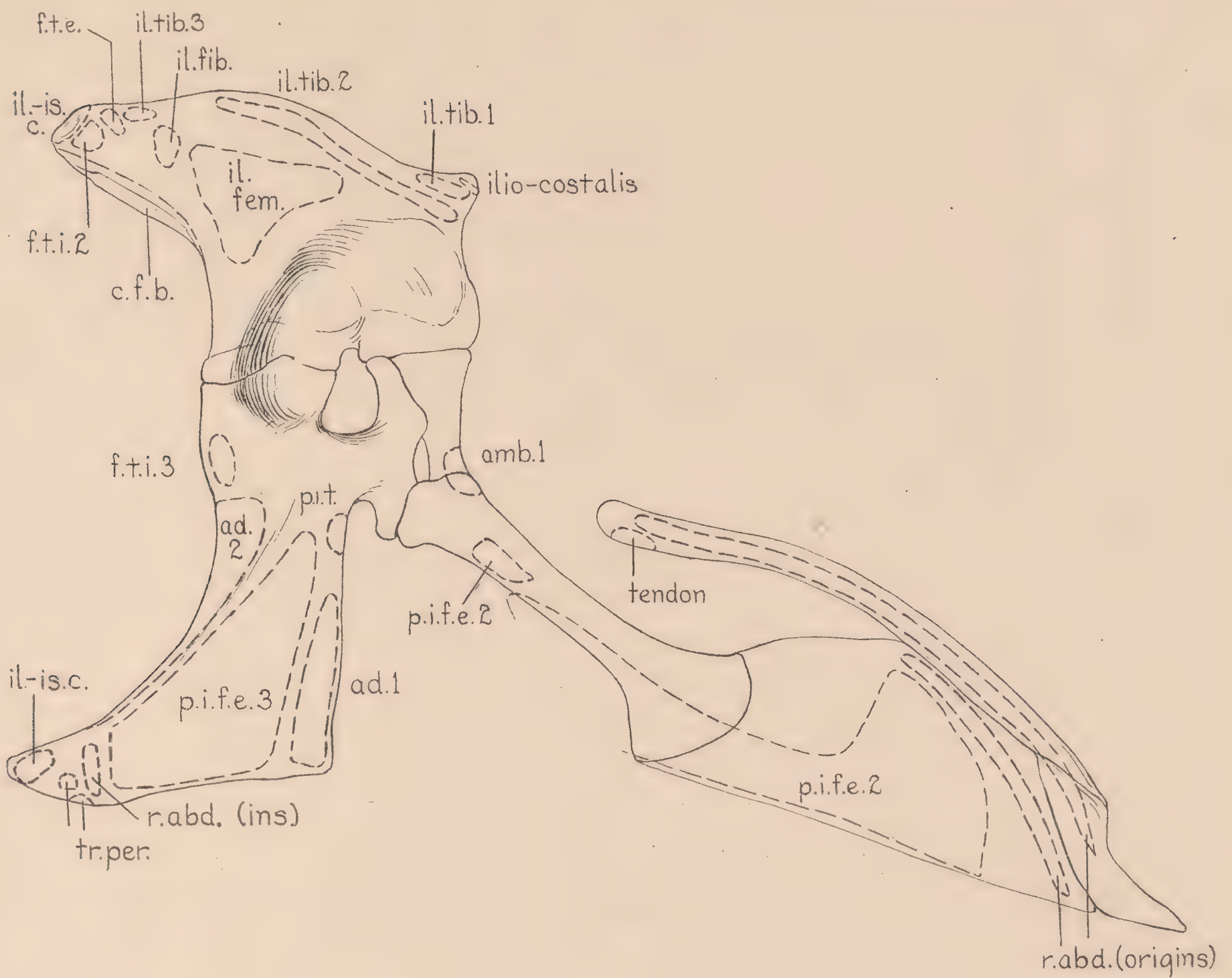




PLATE XXV

Dorsal, anterior, ventral and posterior aspects of the femur, showing muscular attachments.



PLATES XIX to XXV



PLATE XIX

- Fig. 1. Lateral view of pelvic region; the limb is shown as if cut half-way down the femur. (All views are of the right side.)
- Fig. 2. The same, with a portion of the superficial musculature removed.



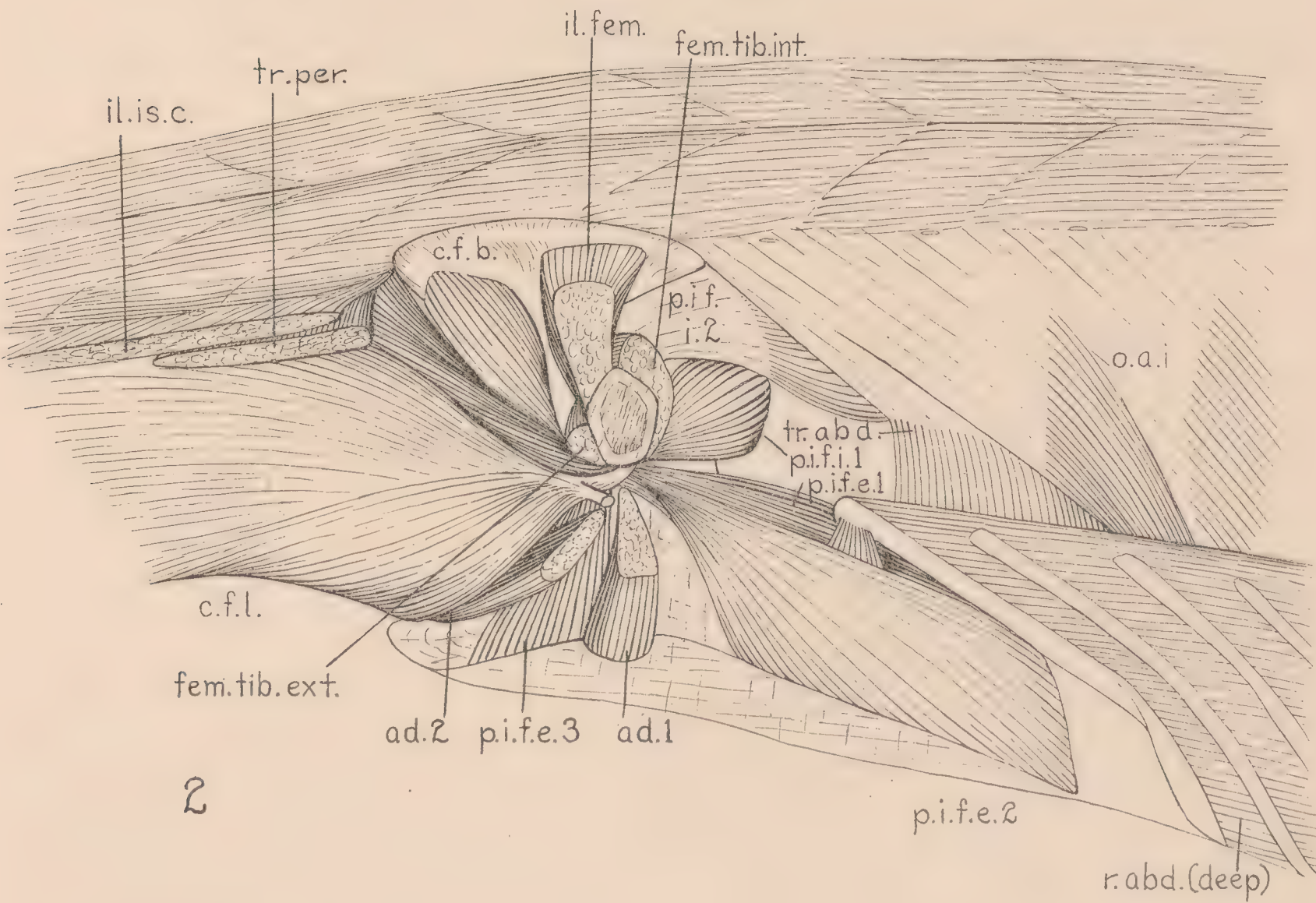
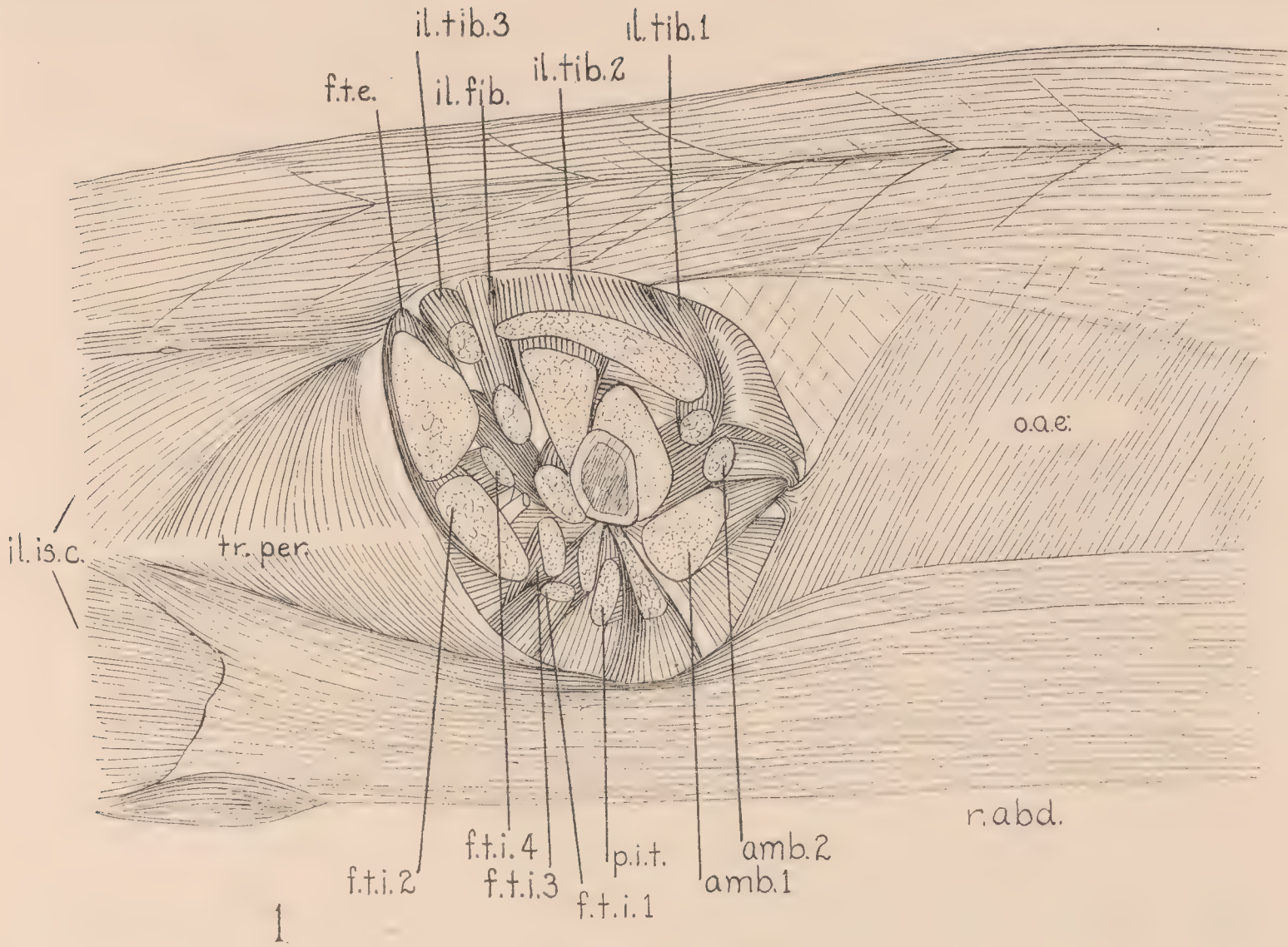




PLATE XX

Fig. 1. Lateral view of the deep musculature of the pelvic region, with most of the muscles shown in Plate XIX removed.

Fig. 2. Inner aspect, through the mid-line ventrally and cut through the sacral ribs dorsally. The dorsalis trunci+caudæ have been removed.



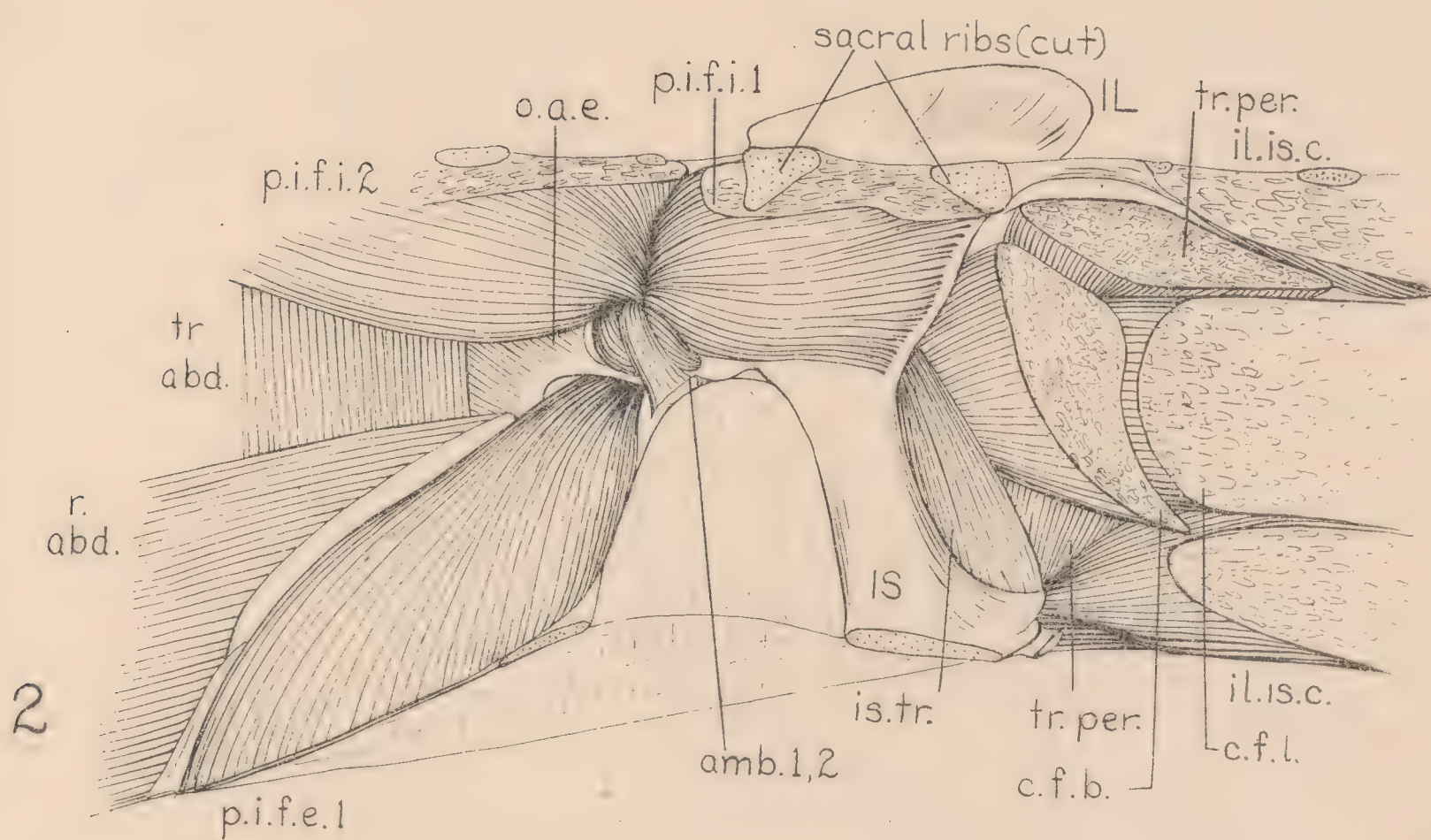
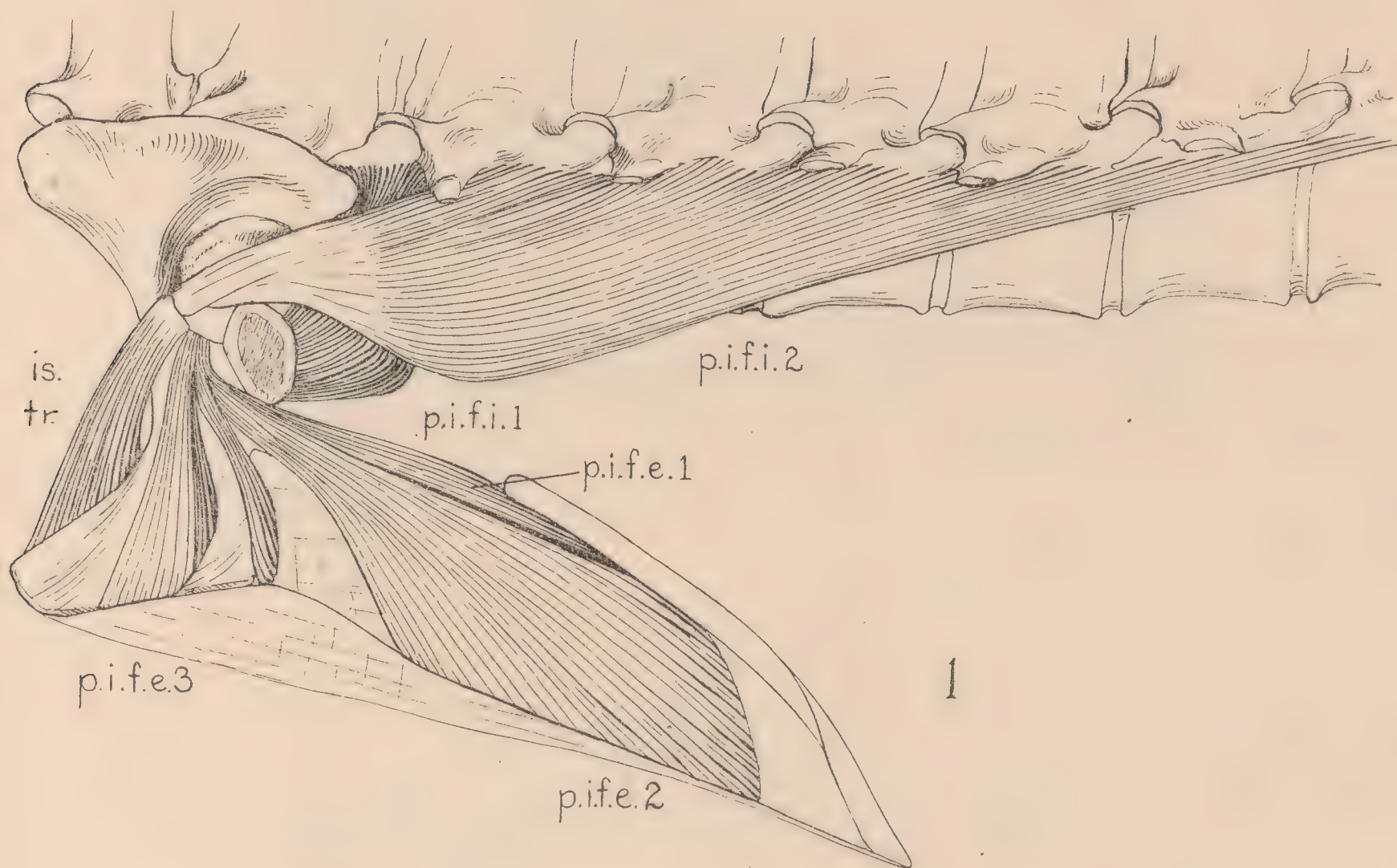
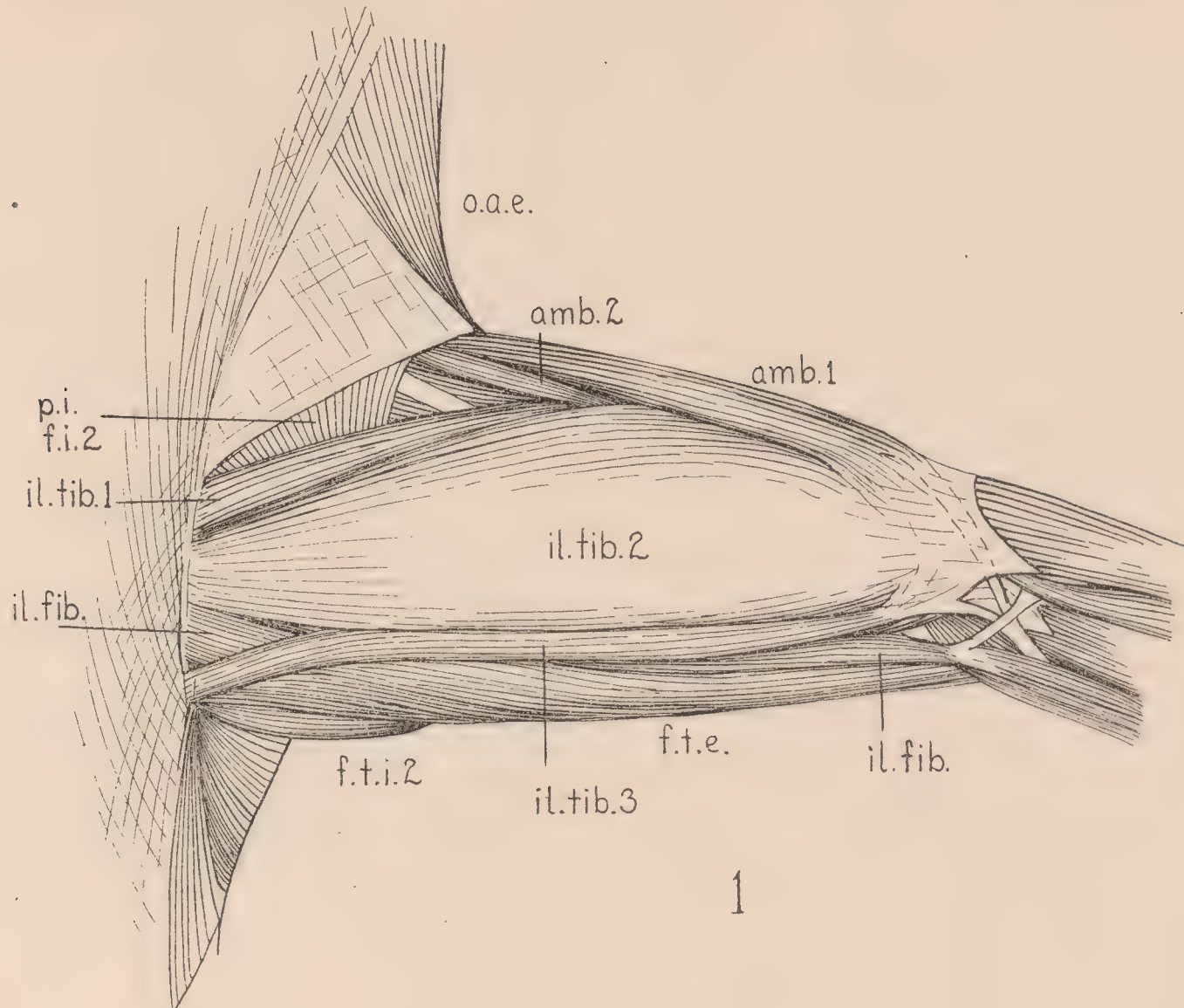




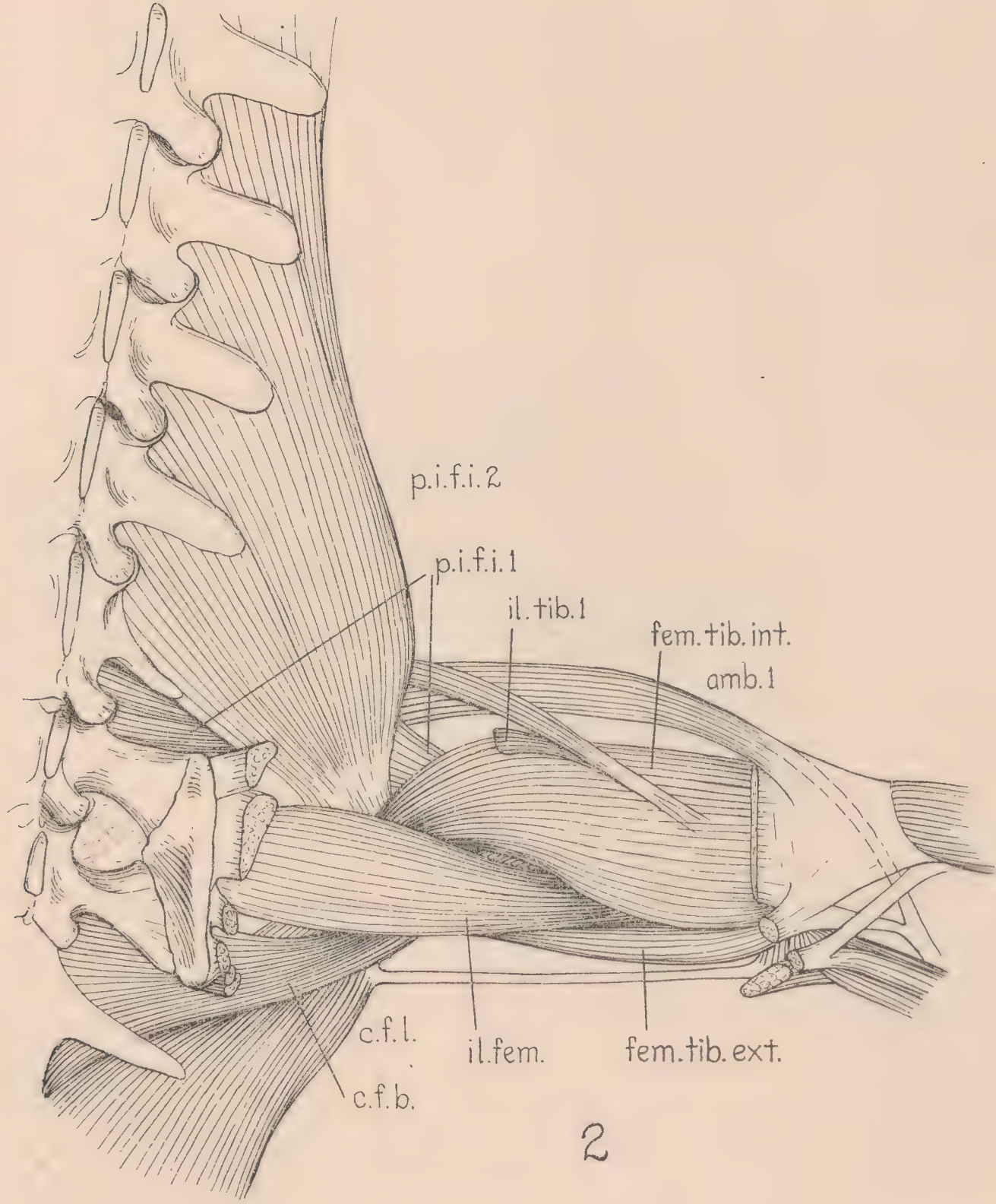
PLATE XXI

- Fig. 1. Superficial dorsal view.  
Fig. 2. Deeper view of the dorsal musculature.





1



2



PLATE XXII

Fig. 1. Dorsal view of pelvic region, with the spinal column and ribs removed, to show the deep musculature.

Fig. 2. Superficial ventral view.



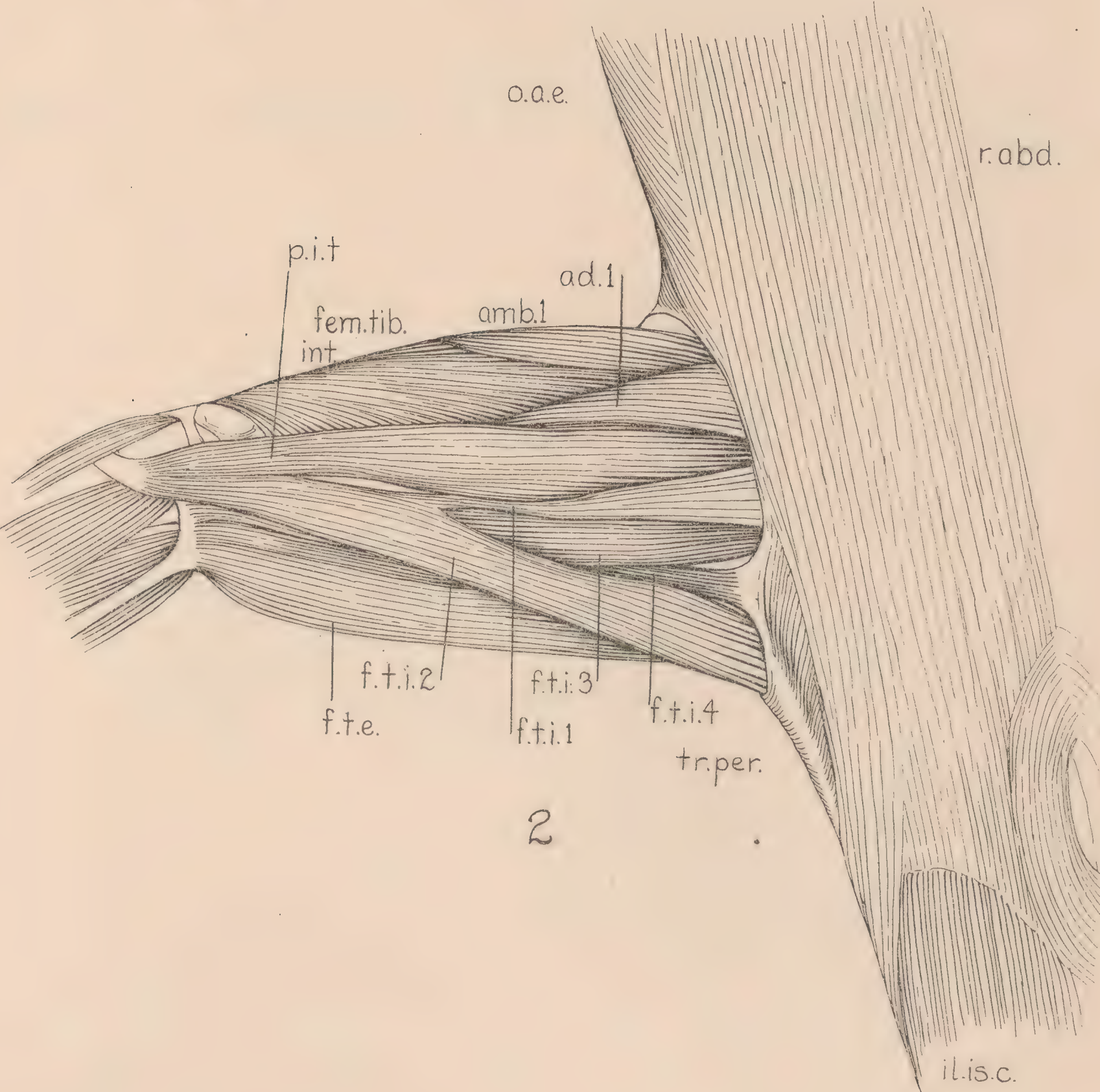
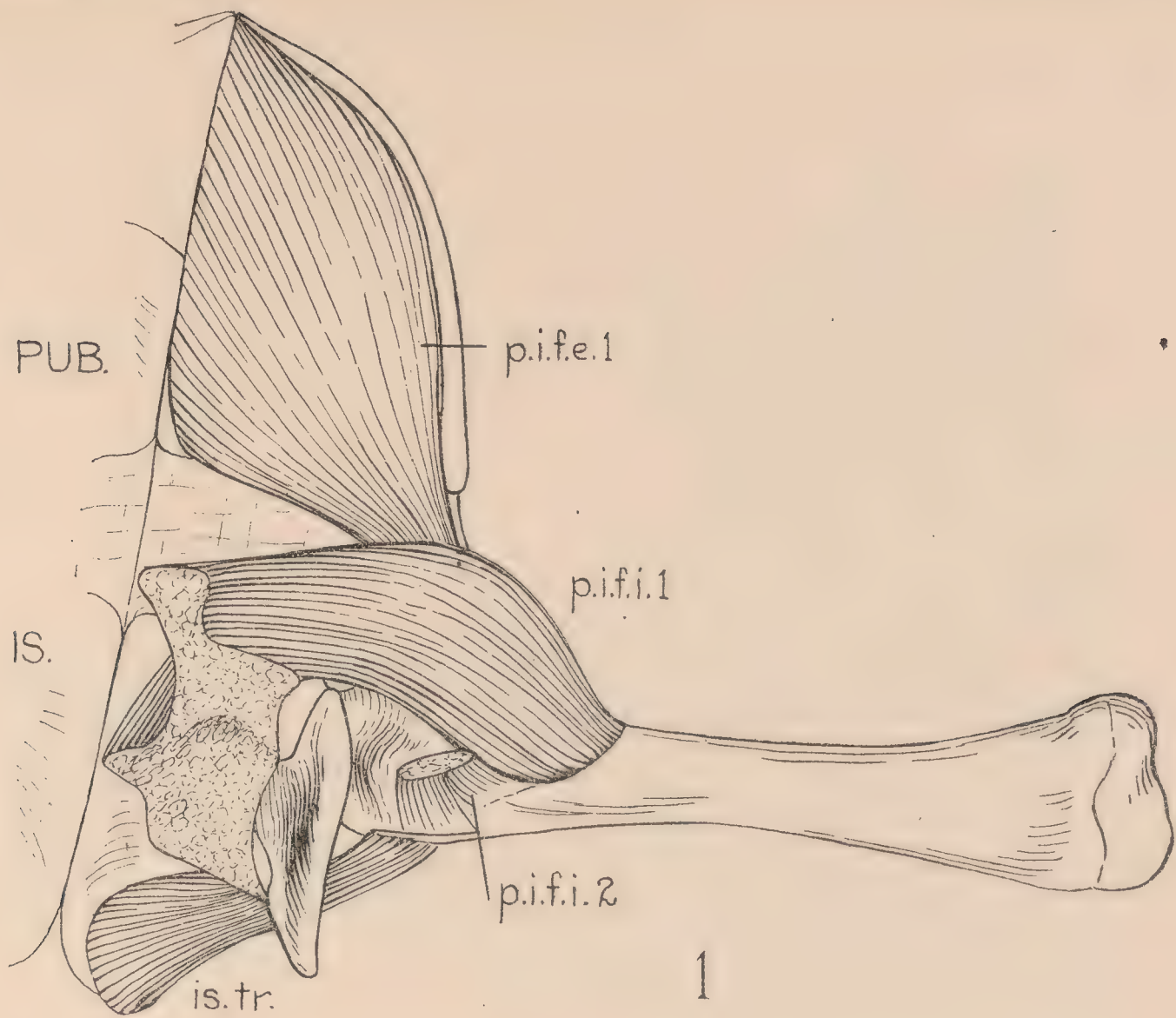




PLATE XXIII

- Fig. 1. Ventral view, with a portion of the axial musculature and the long flexors cut.
- Fig. 2. Deep ventral view.



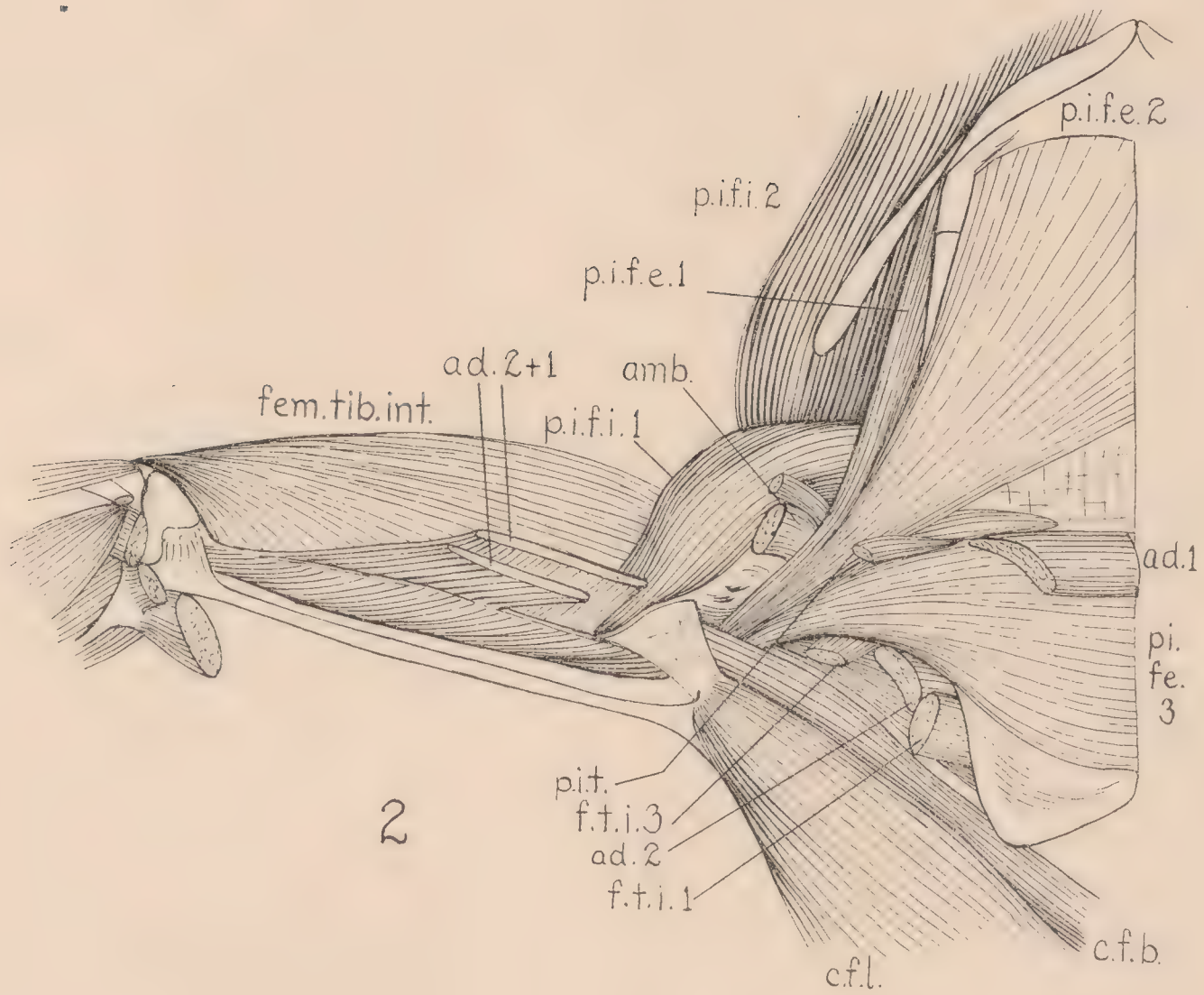
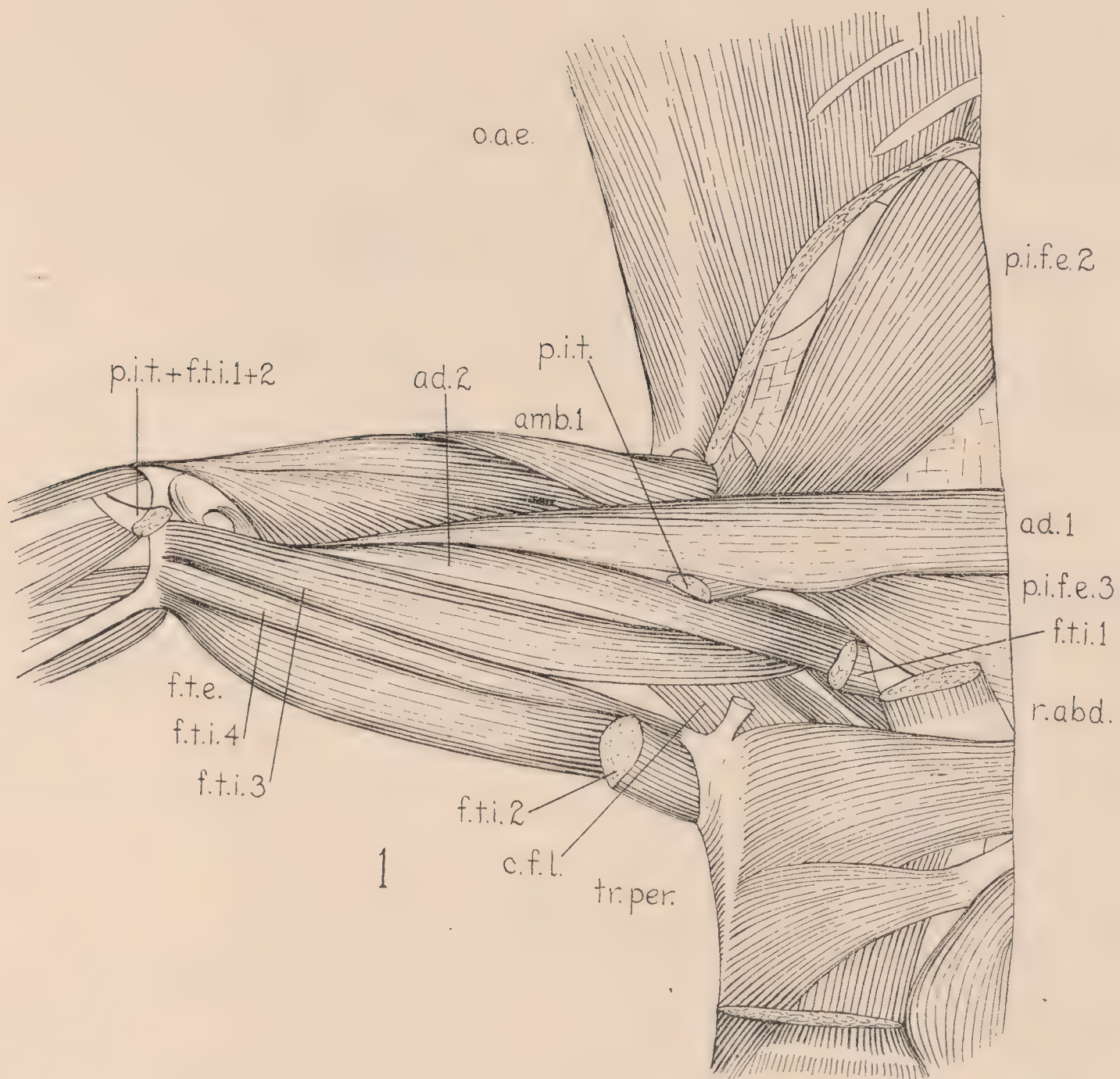
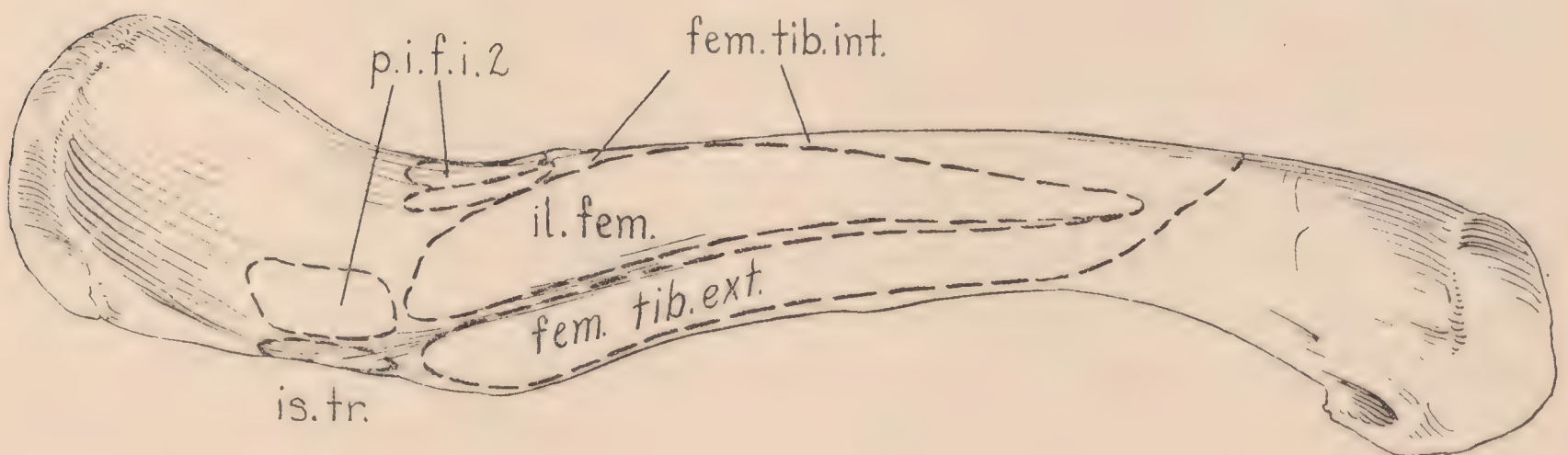
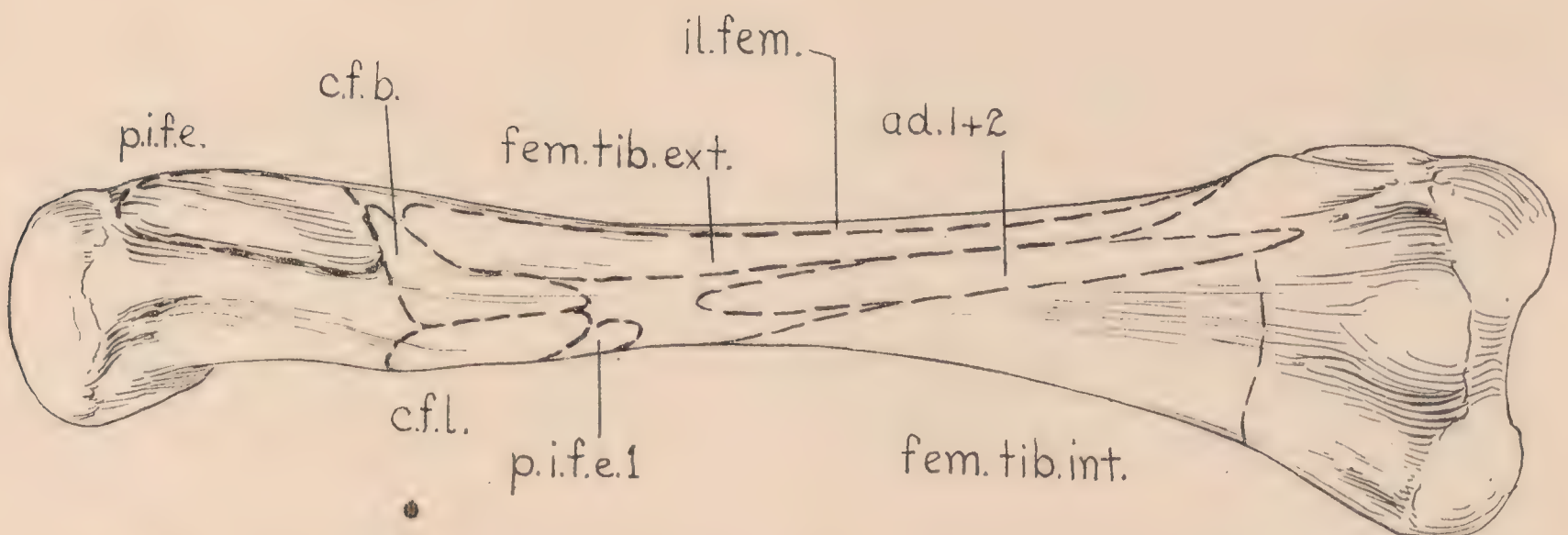
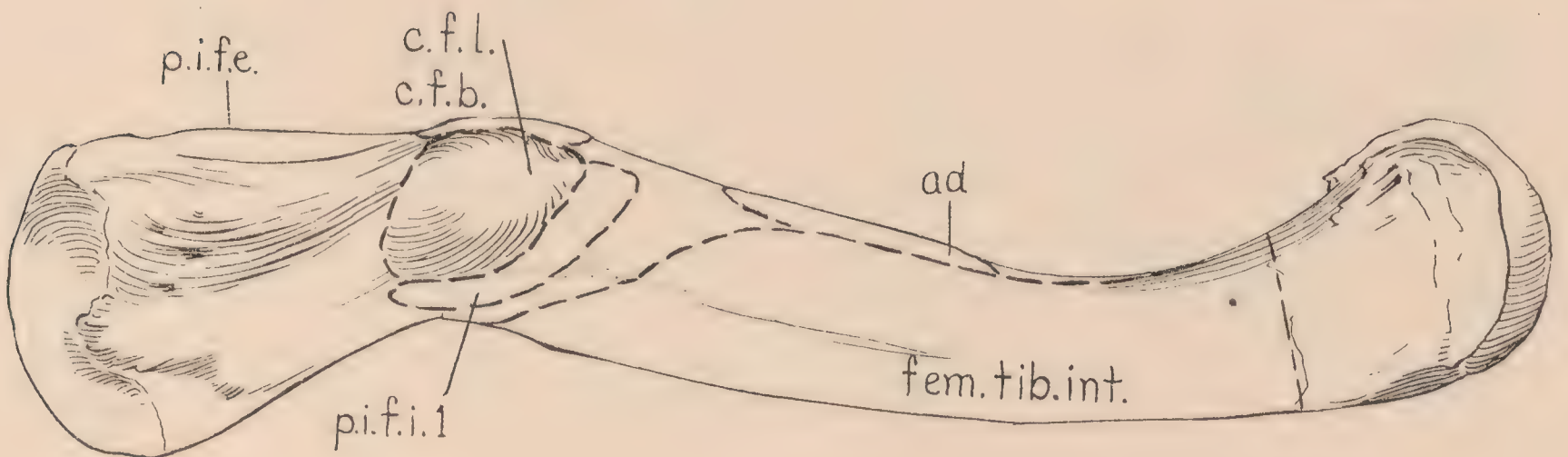
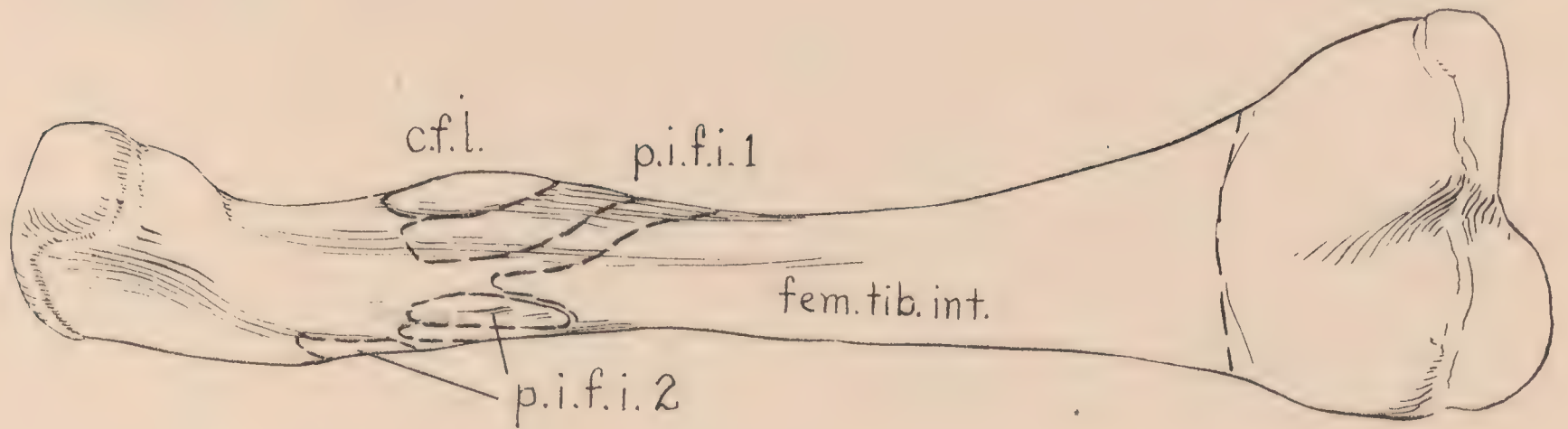




PLATE XXIV

Outer and inner surfaces of pelvic girdle, showing muscle attachments.











**Article XVI.—SKULL CHARACTERS OF *ALLIGATOR SINENSE***  
**FAUVEL<sup>1, 2</sup>**

BY CHARLES C. MOOK

When the skull characters of the recent species of Crocodilia were described by the writer in 1921<sup>3</sup> no skull of *Alligator sinense* was available for study, in consequence of which this species was dismissed with a brief summary of characters taken from Boulenger's 'Catalogue of the Recent Reptilia in the British Museum.'

In 1922 the American Museum received a number of skins, skulls, and skeletons of the Chinese alligator, collected by the Third Asiatic Expedition. This material sheds light upon previously unknown characters of this species and forms the basis of the present communication. This description is based particularly upon one skull (A. M. N. H. No. 23898) and many of the characters have been verified upon three other skulls (A. M. N. H. Nos. 23899, 23900, 23901).

GENERAL FORM

The skull is short and broad. It is relatively shorter than that of *A. mississippiensis* and resembles in this respect the Miocene *A. thomsoni*. The height is greater than in the Florida species.

The snout is moderately broad at its anterior end and expands rapidly to the level of the fourth maxillary teeth, then contracts slightly to the level of the sixth maxillary teeth, back of which it expands again. The length of the snout is one and one-sixth times as long as its breadth at the base.

The interorbital plate is situated at a distinctly higher level than the snout and descends abruptly at its anterior end. A pair of prominent ridges extend forward and outward along the anterior borders of the orbits to points slightly in front of the semi-detached supraorbitals and then extend directly forward over the base of the snout. In this character the skull resembles those of the various species of *Jacare* and that of *A. thomsoni* but differs from that of *A. mississippiensis*. The interorbital plate is relatively narrow and is uprolled at its edges. It is also slightly convex in antero-posterior profile.

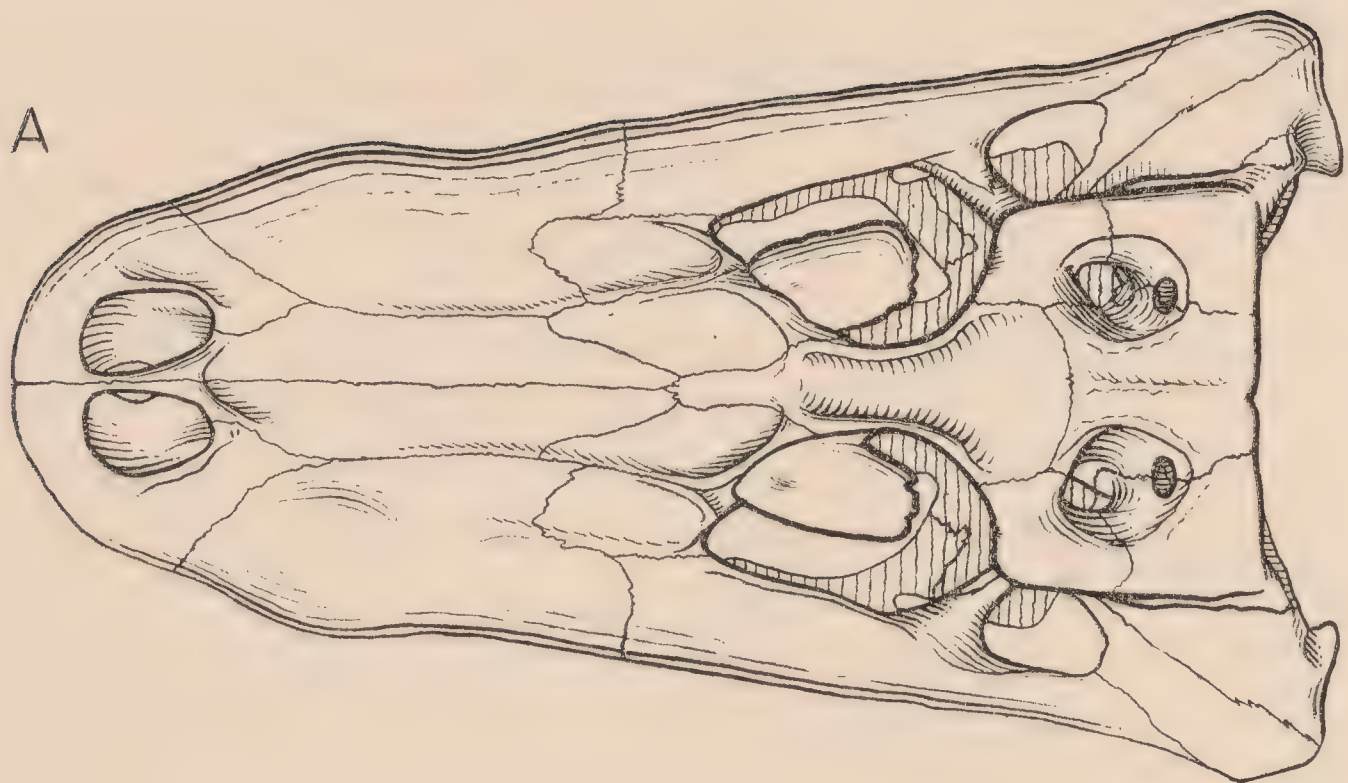
The cranial table is short antero-posteriorly but rather broad laterally. Its lateral borders converge in the anterior direction at such

<sup>1</sup>Contributions to the Osteology, Affinities and Distribution of the Crocodilia, No. 12.

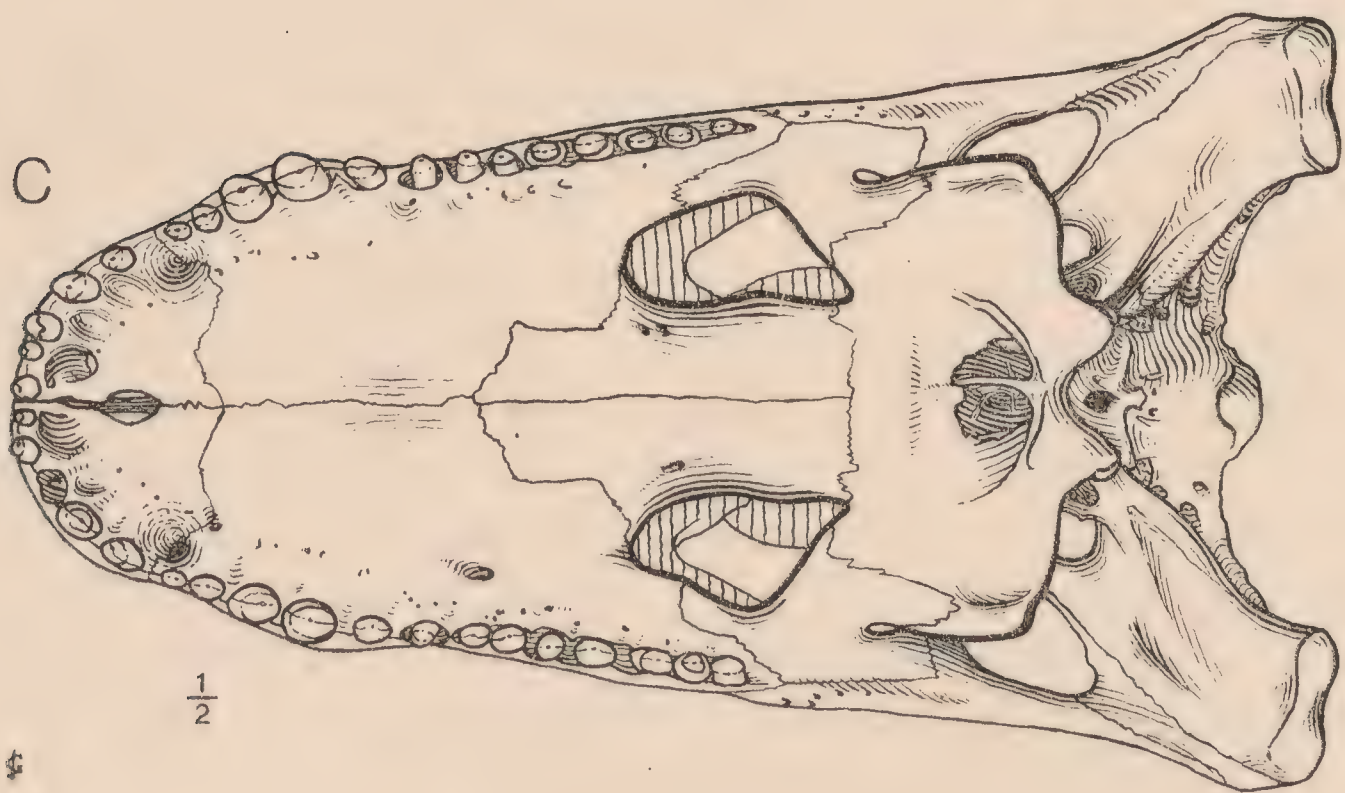
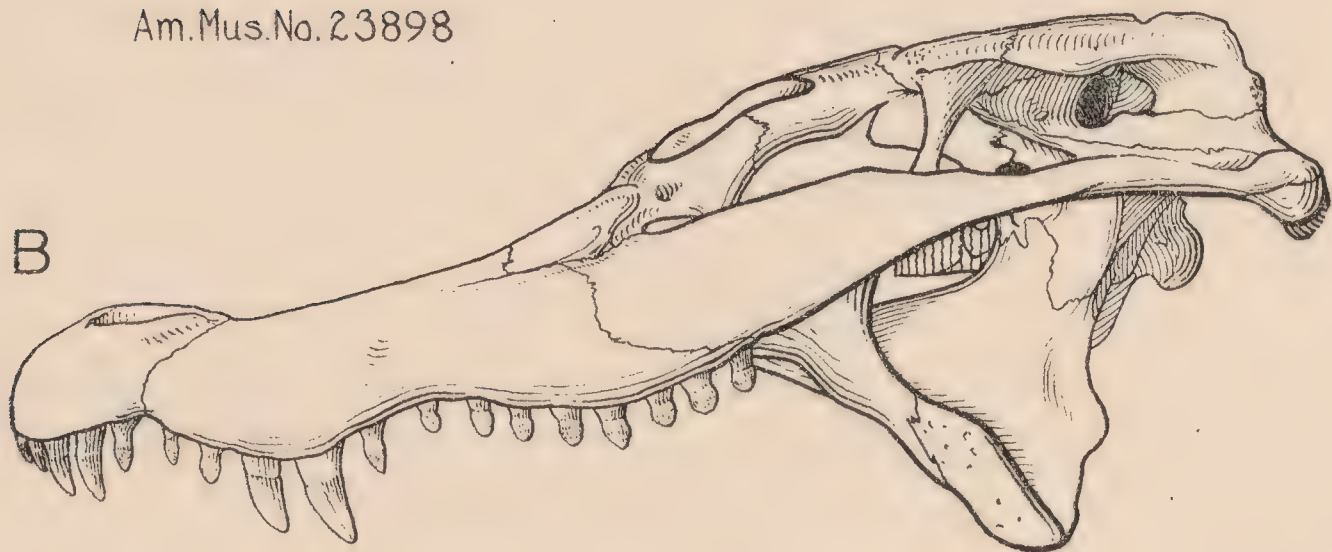
<sup>2</sup>Publications of the Asiatic Expeditions of The American Museum of Natural History. Publication No. 14.

<sup>3</sup>Bull. Amer. Mus. Nat. Hist., XLIV, Art. 13, pp. 123-268.





Am. Mus. No. 23898



$\frac{1}{2}$

Fig. 1. *Alligator sinense* Fauvel.

Skull (Amer. Mus. No. 23898). One-half natural size. A, superior view; B, lateral view, left side; C, inferior view.



an angle that, if produced forward, they would meet slightly beyond the tip of the snout. The plate between the supratemporal fenestræ is of moderate breadth and is distinctly uprolled at its edges. The lateral borders of the skull are more distinctly wavy than in the southern alligator.

#### THE CAVITIES OF THE SKULL

**SUPRATEMPORAL FENESTRÆ.**—The supratemporal fenestræ are large at the surface of the cranial table but diminish rapidly in size in depth. Viewed from above, less than half of the area of each fenestra penetrates to the base of the brain-case. The larger part, chiefly posterior, is very shallow and is floored by portions of the parietal and squamosal bones. The small internal cavities which extend from the supratemporal fenestræ to the aural passages are in most crocodilians nearly or quite invisible when the skull is viewed from above; in this species they are entirely visible from above. The edges of the fenestræ are distinctly uprolled, especially on the postero-internal borders. In this character they differ from those of *A. mississippiensis* and *A. thomsoni*. In shape the fenestræ are irregular and not smoothly rounded. Their outlines end posteriorly in rather blunt points and anteriorly, or rather antero-externally, in sharp points. There is a certain amount of variation among the various individuals in regard to this character. The space between the fenestræ is relatively broad.

**INFRATEMPORAL FENESTRÆ.**—These fenestræ are of moderate size. Their chief point of interest is that their triangular outline is more rounded than in most crocodilians.

**ORBITS.**—The orbits are large. They are irregular in outline; their posterior and postero-internal borders are broadly rounded; their antero-internal borders are nearly straight, as are their external borders. They end anteriorly in rather sharp points, which are nearer their external than their internal boundaries. The length of the orbits is considerably greater than their breadth. The interorbital plate is of moderate breadth; its borders are sharply uprolled. In all of the specimens the anterior ends of the orbits lie over several maxillary teeth. This character indicates immaturity in all of them.

**EXTERNAL NARES.**—The external narial aperture is broader than it is long. The bony bar which divides it into right and left elements at the surface is moderately stout. It is composed chiefly of the anterior processes of the nasals, but partly of processes of the premaxillaries. In outline the cavity is a somewhat rounded quadrilateral, whose anterior



border is slightly curved and whose lateral borders converge slightly in the posterior direction. The posterior border is very irregular. The lateral borders are distinctly elevated above the general level of the anterior end of the snout. The median bar is also elevated and the posterior border slightly so.

PREMAXILLARY FORAMEN.—This foramen is very small; on the median line it occupies less than one-third of the distance between the tip of the snout and the premaxillo-maxillary suture. It is acutely pointed at both anterior and posterior ends and its lateral borders are simple curves.

PALATINE FENESTRÆ.—The palatine fenestræ are small and are very irregular in shape. In this the species differs from *A. mississippiensis*. The internal borders are nearly straight parallel lines throughout the posterior two-thirds of their lengths; the anterior thirds diverge rapidly. The external borders are composed of two components of about equal length, which make pronounced angles with each other slightly posterior to the level of the last maxillary teeth. About one-fifth of each external border consists of maxillary bone, the ectopterygoid portion comprising nearly four-fifths, with a minute portion at the posterior end consisting of pterygoid; the entire internal border is composed of palatine. The maximum breadth is considerable in proportion to the maximum length. The anterior end is broadly rounded but the posterior end is acute. The anterior end is situated at the level of the space between the tenth and eleventh maxillary teeth.

INTERNAL NARIAL APERTURE.—This aperture is completely divided by a median vertical plate. On its anterior border at the median line is situated a slight but distinct elevation. Posterior to the aperture is a prominent vertical ridge, approximately semicircular in outline, which completely separates the depression, of which the aperture is the center, from the postero-external elevated flanges of the pterygoid bone.

#### THE BONES OF THE SKULL

PREMAXILLARIES.—The premaxillaries are considerably broader in proportion to their length on their superior surfaces than in the Florida alligator. Their posterior processes are of moderate length, extending backward from the level of the second to that of the fourth maxillary teeth. A small process of both premaxillaries extends backward from the anterior end of the narial aperture to meet the anterior process of the nasals, as in *A. mississippiensis*. The edges of the premaxillaries forming the lateral borders of the aperture are turned sharply upward however,



differing in this character from those of the Florida species. The posterior end of the narial aperture is situated farther back than in the latter species with respect to the level of the premaxillo-maxillary sutures at the lateral borders of the skull.

On the palate the proportion of length to breadth is the same as in the Florida alligator. There are two deep pits on each side, one posterior to the space between the first and second teeth, the other at the premaxillo-maxillary suture. The first of these lodged the first mandibular tooth, the second, the fourth mandibular tooth. On the median line the distance from the anterior end of the premaxillary foramen to the anterior border of the skull is equal to the distance from the posterior end of the foramen to the premaxillo-maxillary suture.

The suture between the premaxillaries and the maxillaries differs from that of *A. mississippiensis*. It extends inward and backward from the external border, across the pit for the fourth mandibular tooth, to a point half-way between the external border and the median line and at the level of the space between the first and second maxillary teeth; from this point it extends inward and slightly forward half-way to the median line, then turns inward and backward and meets the median line at the level of the spaces between the first and second maxillary teeth. From the median line it extends in a symmetrical direction to the opposite border of the skull. The entire suture is therefore wavy in outline.

Each premaxillary contains five teeth, of which the fourth are the largest, the third second in size, the fifth third in size and the first and second very small. The teeth are evenly spaced.

MAXILLARIES.—These bones are short and broad. They are especially short along the sutures with the nasals; these sutures are less than one-fifth as long as the skull, in contrast to over one-fourth in a Florida alligator of slightly larger size. The sutures with the prefrontals are exceedingly short, being about one-fourth the length of the maxillo-lacrymal sutures. In the Florida alligator they are over one-half the length of the maxillo-lacrymal sutures. The sutures with the jugals are long, especially in their transverse portions. On the palate the maxillaries are especially short and broad. Comparison with a small skull of *Alligator mississippiensis* may be expressed as follows.



|                                        | <i>A. sinense</i> A. M. N. H.<br>No. 23898 | <i>A. mississippiensis</i><br>A. M. N. H. No. 12572 |
|----------------------------------------|--------------------------------------------|-----------------------------------------------------|
| <u>Length maxillaries, median line</u> | .215                                       | .295                                                |
| Length skull                           |                                            |                                                     |
| <u>Length maxillaries, median line</u> | .444                                       | .500                                                |
| Maximum length, maxillaries            |                                            |                                                     |
| <u>Length maxillaries, median line</u> | .451                                       | .720                                                |
| Maximum breadth, maxillaries           |                                            |                                                     |
| <u>Length maxillaries, median line</u> | .682                                       | .968                                                |
| Length palatines, median line          |                                            |                                                     |

Each maxillary contains thirteen teeth, of which the fourth is the largest and the third is second in size. The first and second maxillary teeth are moderately stout and moderately sharp; the crowns of the posterior teeth are all small. The first six teeth are spaced moderately and evenly; the last seven are close together. In the largest skull studied (A. M. N. H. No. 23898) the first six maxillary teeth have separate alveoli and the last seven are lodged in a common alveolar groove. In smaller skulls, however, not at present thoroughly cleaned, the posterior teeth, or at any rate, some of the posterior teeth, appear to have separate alveoli.

NASALS.—These bones are very short; on the median line they occupy considerably less than one-half the length of the skull. The anterior process, extending forward into the narial aperture, is moderately broad at its base and very narrow where it joins the process of the premaxillaries, extending back from the anterior border of the narial aperture. From the posterior border of the narial aperture the nasals broaden rapidly to the posterior extremities of the premaxillaries, which is the point of their greatest breadth. From this point back they narrow gradually to the anterior ends of the naso-prefrontal sutures, back of which they narrow rapidly to their blunt posterior extremities, which are situated slightly forward from the level of the anterior ends of the orbits. The sutures with the maxillaries are relatively short; those with the prefrontals are relatively long.

PREFRONTALS.—The prefrontals are moderately long. Their anterior ends extend forward as narrow processes, wedging apart the nasals and lacrymals and to a slight extent the nasals and maxillaries. Their contacts with the lacrymals are somewhat elevated into ridges and their orbital borders are greatly elevated, to a slight extent even overhanging. Their posterior processes are short and their contacts with the frontal are moderately so.



LACRYMALS.—The lacrymal bones are relatively short and broad. Each suture with the prefrontal extends in a line which is almost parallel with the median line but which is inclined very slightly toward the median line in the anterior direction. The sutures with the maxillaries extend forward and outward irregularly from the anterior ends of the prefronto-lacrymal sutures to points near the external boundaries of the bones, then slightly outward and backward to join the straight lacrymo-jugal sutures. A small but conspicuous oblique ridge extends outward and forward from the postero-internal corner of each lacrymal to the center of the lacrymo-jugal suture, separating a small, low, smooth orbital surface from the more elevated pitted surface. The anterior extremities of the lacrymals are situated farther forward than those of the prefrontals. In this character the species differs from *A. mississippiensis*.

FRONTAL.—The anterior process of the frontal is smooth and is relatively short. It does not wedge apart the nasals at their posterior extremities but ends abruptly. The interorbital portion is narrow and is decidedly uprolled at the edges. The pitting is arranged in such a manner in this portion of the bone as to leave a distinct but slight median ridge. The posterior portion is relatively broad. The sutures with the postorbitals are very short; the suture with the parietal is a simple curve, the convexity being directed backward. The frontal is entirely removed from the supratemporal fenestræ, thus differing somewhat from that of the Florida alligator.

POSTORBITALS.—The postorbitals are slightly longer than broad; in *A. mississippiensis* they are considerably longer than broad. They also differ from those of the latter species in occupying a larger proportion of the external border of the cranial table.

SQUAMOSALS.—The proportion of the breadth to the length of the squamosals is greater than in the Florida alligator, and the sutures of these bones with the parietal are less symmetrically curved than in the latter species.

PARIETAL.—This bone occupies a considerable portion of the surface of the cranial table anterior to the supratemporal fenestræ as well as posterior to them. It occupies nearly a third of the posterior border of the cranial table. Its interfenestral plate is relatively broad, compared with *A. mississippiensis*. It is somewhat uprolled at its external, or fenestral, borders. A low median ridge serves to distinguish it readily from that of the American species.



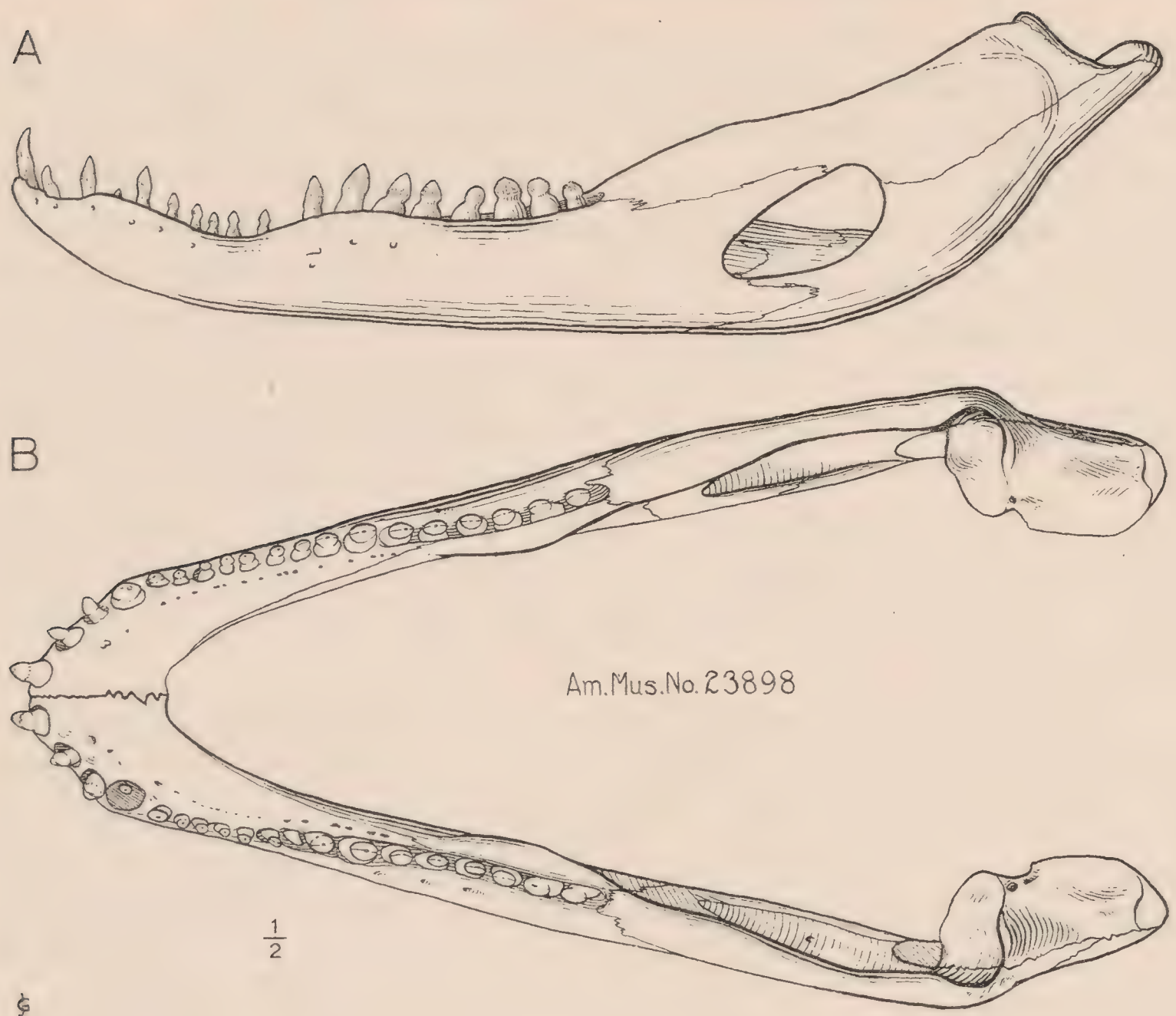


Fig. 2. *Alligator sinense* Fauvel.

Mandible (Amer. Mus. No. 23898). One-half natural size. A, lateral view, left side; B, superior view.

**SUPRAOCCIPITAL.**—As in *A. mississippiensis* this bone occupies no portion of the border of the cranial table. On the posterior surface of the skull it is narrow laterally and deep vertically. It extends downward to a point about four-fifths of the total distance from the foramen magnum to the cranial table, below the latter.

**EXOCCIPITALS.**—These bones are relatively deep in the vertical direction. They comprise small portions of the occipital condyle.

**BASIOCCIPITAL.**—This bone comprises most of the occipital condyle but not all of it.

**BASISPHENOID.**—This bone is not especially characteristic.

**QUADRATES.**—The quadrates are stout in proportion to their length and their articular surfaces are unusually broad.

**QUADRATO-JUGALS.**—These bones do not differ from those of *A. mississippiensis* in any characteristic way.

**JUGALS.**—The jugals are relatively larger than in the Florida species and differ from those of the latter in form. Their length is over half the



total length of the skull and they occupy a large portion of the lateral surface of the skull. Their posterior processes are slender, as in the American form, but the anterior processes are much greater than in the latter. The maximum height of each jugal in *A. mississippiensis* is considerably behind the posterior end of the maxillary, near the posterior end of the orbit; in *A. sinense* it is over the posterior process of the maxillary, near the level of the anterior end of the orbit. The suture with the maxillary differs considerably from that in the Florida alligator.

**PALATINES.**—The palatines of this species differ considerably from those of *A. mississippiensis* and in fact of all other crocodilians. Their sutures with the maxillaries extend inward and slightly forward from the anterior ends of the palatine fenestræ about half-way to the median line, then turn directly forward or with a gentle curve whose concavity faces outward to the level of the eighth maxillary teeth, then either directly inward (A. M. N. H. No. 23899) or inward and forward (A. M. N. H. No. 23898) to meet at the median line. The interfenestral portions are very broad and their fenestral borders are nearly parallel. Their pterygoid borders form a nearly straight line.

**PTERYGOIDS.**—The pterygoids are not especially distinctive. They are considerably arched and the ridge back of the internal narial aperture is unusually high. The aperture is divided, as in the Florida species.

**ECTOPTERYGOIDS.**—These bones are very short antero-posteriorly and are very stout.

**THE MANDIBLE.**—The mandible is relatively broader in proportion to its length than in the Florida alligator, the rami diverge at a relatively sharper angle, and the individual elements are all stouter. The symphysis extends back to the level of the fifth mandibular teeth, contrasting with the short symphysis reaching only slightly back of the level of the third in the American species. The splenials do not enter the symphysis but extend forward within a relatively minute distance of it; this is in contrast with the wide spaces between the anterior ends of the splenials and the symphysis in *A. mississippiensis*.

The dental borders occupy about half the length of the mandible, an unusual condition among the living crocodilians, probably approached only by *Jacare latirostris*. There are nineteen teeth in each ramus. The fourth is the largest of these and the thirteenth is second in size. The first teeth are moderately large and are widely separated from the smaller second, which are widely separated from the equal-sized third, which are moderately far from the fourth. Back of the fourth are seven small teeth close together. Back of the thirteenth the short blunt teeth are



all close together. The variation in the size and the arrangement of the teeth is quite different from that in *A. mississippiensis*.

The external mandibular foramen is relatively high in proportion to its length. Its surangular border is longer than in the American form. The internal mandibular foramen is relatively small.

#### DISCUSSION

This species resembles the living Florida alligator very closely in some respects but differs from it quite markedly in others.

It has certain resemblances to the various species of *Jacare* which are absent in *A. mississippiensis*. These resemblances are offset by other more fundamental characters, however, and there is no evidence of close relationship.

The nearest approach to the structure of this species is to be seen in the Miocene *Alligator thomsoni*, recently described by the writer.<sup>1</sup> The species may therefore be considered more primitive than *A. mississippiensis*, though it has some specializations absent in the latter. *A. thomsoni* approaches *Allognathosuchus polyodon* from the Bridger, which in turn approaches *Allognathosuchus heterodon* of the Wasatch in a number of characters, so that we may consider the following as a logical morphological sequence: *Allognathosuchus heterodon* (Eocene); *Allognathosuchus polyodon* (Eocene); *Alligator thomsoni* (Miocene); *Alligator sinense* (Recent); *A. mississippiensis* (Recent). This does not necessarily indicate a line of descent, but it does indicate that *Alligator sinense* serves partially to bridge the wide structural gap between *A. mississippiensis* and the earlier Tertiary crocodilians. *A. mississippiensis* has been found in Pleistocene deposits. We await the discovery of *A. sinense*, or a very closely related form, in Pleistocene, or even Pliocene, deposits.

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<sup>1</sup>Amer. Mus. Novitates, No. 73.



Article **XVII.**—NEW FOSSIL MAMMALS FROM THE PLIOCENE  
OF SZE-CHUAN, CHINA<sup>1</sup>

BY W. D. MATTHEW AND WALTER GRANGER

The following is a preliminary notice of a collection secured during the winter of 1920–1921 by Mr. Walter Granger, palæontologist of the Third Asiatic Expedition sent out by the American Museum, the American Asiatic Association, and Asia Magazine, under leadership of Mr. Roy C. Andrews. The locality is a series of pits or fissures at the village of Yen-ching-kao in the vicinity of Wan-hsien, province of Sze-chuan. These pits have been worked by the natives for many years for the Chinese drug trade. Mr. Granger's account of their occurrence and stratigraphic observations and more extended descriptions of the fauna will be published later, this notice serving to place certain interesting novelties upon record.

The age of the fauna is provisionally placed as Upper Pliocene on account of the abundance of *Stegodon* remains and absence of any higher type of Proboscidean, but its final correlation is left open for the present.

The Chinese fossil mammals described by Owen in 1870<sup>2</sup> came from "a cave near the city of Chung-king-foo in the province of Sze-chuan." Chung-king is on the Yang-tse-kiang above Wan-hsien, about one hundred and forty miles distant in an air line. If correctly reported by the finders, Owen's specimens could hardly have come from the Yen-ching-kao pits; but it is apparently the same fauna, or at all events of similar facies and doubtless the same conditions of preservation. Possibly the Chinese informants of Consul Swinhoe, who sent the fossils to Owen, misled him, unintentionally or deliberately, as to the locality. This point will be further discussed at a later date. Owen regarded the fauna as Pliocene and described the following species:

|                                |                                      |
|--------------------------------|--------------------------------------|
| <i>Stegodon orientalis.</i>    | Parts of molars.                     |
| <i>Rhinoceros sinensis.</i>    | Parts of 4 upper and 4 lower molars. |
| <i>Tapirus sinensis.</i>       | Parts of 3 upper and 4 lower teeth.  |
| <i>Chalicotherium sinense.</i> | Part of an upper molar.              |
| <i>Hyæna sinensis.</i>         | Canine, 2 premolars.                 |

<sup>1</sup>Publications of the Asiatic Expeditions of The American Museum of Natural History, Publication No. 15.

<sup>2</sup>Quar. Journ. Geol. Soc., London, XXVI, pp. 417–436, Pls. xxvii–xxix.





3  
8

A. M. 18628

Fig. 1. *Rhinoceros sinensis* Owen. Amer. Mus. No. 18628. Palate of neotype skull. Natural size.



The first three genera are among the most abundant types of large animals in the Yen-ching-kao pits. *Chalicotherium* and *Hyæna* are rare. Owen's descriptions and figures accord very well with some of the species in our collection, so that we have referred them to his species, whether or not later investigation proves them to be exact topotypes.

Koken in 1885<sup>1</sup> described a collection secured by von Richthofen, apparently from the trading junks of the Yang-tse-kiang and understood by him to have come from far up the river in "caves in Yun-nan." Whether this was the real locality remains to be verified; one has the impression from the reading of von Richthofen's letter, quoted by Koken, that the traveller himself suspected that the locality might not have been correctly stated. It is certain at all events that the major part of Koken's collections, like Owen's, represent substantially the same faunal facies, and they seem to agree as to species, in part at least, with our collections. Koken also distinguishes an older fauna of supposed Lower Pliocene age, including *Hipparion*, *Camelopardalis*, *Palæomeryx*, etc., which is more extensively represented in Schlosser's later collections, and is probably substantially the same fauna as the fine collections secured recently by J. G. Andersson<sup>2</sup> and now being studied by Professor Wiman.

Schlosser in 1903<sup>3</sup> described a large collection secured by Dr. Haberer for the Munich museum, and revised the work of Owen, Koken and other previous writers. He concluded that Owen's fauna, except *Stegodon*, and most of Koken's material, was of Pleistocene age. There is no doubt, however, that the *Stegodon* is coeval with the rest of the fauna in Granger's collection, and one may assume that it was probably so in the Owen and Koken collections. Schlosser's material belonged mostly to the older Pliocene fauna distinguished by Koken and came from localities farther to the north.

The collections from Sze-chuan described by Professor Matsumoto, in 1915<sup>4</sup> may have come in large part or all from the Yen-ching-kao pits; he does not state any exact localities, but the correspondence of the fauna is evident. Matsumoto divides the material studied by him into two faunas, one found in brown clay and more strongly petrified, the other in cave-loam, feebly fossilized and the teeth strongly colored. The former includes *Stegodon*, *Aceratherium hipparionum*, *Proboselaphus watasei* and *liodon*, *Bibos geron* and two unnamed species of *Buffelus*. The latter includes *Hyæna ultima*, *Rhinoceros sinensis* and *R. plicidens*.

<sup>1</sup>Koken, E. 1885. 'Fossile Säugethiere aus Chinas.' Pal. Abh., III, Heft 2.

<sup>2</sup>Andersson, J. G. 1922. Bull Amer. Mus. Nat. Hist., XLVI, pp. 727-737.

<sup>3</sup>Schlosser, Max. 1903. 'Fossile Säugethiere Chinas.' Abh. k. bayer. Akad. Wiss., XXII, Abt. 1

<sup>4</sup>Matsumoto, H. 1915. Science Reports, Tohoku Imp. Univ., Second Ser. (Geol.) III, No. 1, pp 1-28, Pls. I-X.





Fig. 2. *Rhinoceros sinensis*. Front of skull and jaws, No. 18626, young individual with milk dentition, the last molar not yet emerged and the second unworn. Natural size.



He regards the first as Upper Pliocene, the second as Lower Pleistocene. In our collections the *Stegodon* material was limited to certain pits occurring low down on the slopes of the mountain valley, and did not occur in pits higher up on the mountain; but we are provisionally disposed to regard this as a matter of limitation of range, and to consider the material from all the pits as of substantially the same geologic age.

Professor Matsumoto's researches<sup>1</sup> upon this and related faunas have been of peculiar value to us as a guide in searching for the probable affinities and identifications of our material.

The Granger collection includes skulls, jaws and numerous parts of jaws of *Stegodon* and *Tapir*, incomplete skulls and many jaws of *Rhinoceros*, a tooth of *Chalicotherium* and a large series of other animals, including a large bovid, smaller antelopes and two or three deer, a pig, various carnivora and a very abundant rodent.

The following notes upon certain described species are a necessary preliminary to the discussion of our new collections.

#### ***Stegodon orientalis* Owen**

Schlosser regards this species as identical with *S. insignis* of India, basing the reference upon the fragmentary teeth described by Owen. Matsumoto regards it as distinct, upon the evidence of the referred material which he describes and figures. The Yen-ching-kao material includes a fairly complete adult skull, two young skulls, a series of palates and lower jaws and many teeth. It should enable us to estimate the affinities of the species more exactly when it has been cleaned up and studied.

#### ***Rhinoceros sinensis* Owen**

Schlosser in his masterly review recognizes this species as valid and considers it most nearly related to *platyrhinus* of the Siwaliks and to the Atelodine group of Pleistocene and modern times. It was, however, practically absent from his Chinese collections at Munich, which seem to have come mostly from the "red clays" of Shan-si, Shen-si and Sze-chuan, but as they were not observed in place the real character and age of the formations remain doubtful. Probably they are chiefly Lower Pliocene. Most of the rhinoceros teeth he refers to *R. habereri*, related in his opinion to *R. palæindicus* and thus to the typical modern *Rhinoceros* of India.

Matsumoto appears disposed to assign *R. sinensis* to the *Teleoceras* group; but if our material be correctly referred, the affinities of Owen's

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<sup>1</sup>Matsumoto, H. 1915, *loc. cit.*; 1921, *idem*, V, No. 3, pp. 75-91, Pls. XIII-XIV.





Fig. 3. *Stegodon orientalis* Owen. No. 18630, adult skull, laterally crushed. One-fifth natural size.





Fig. 4. *Stegodon orientalis*. No. 18640. Young skull and lower jaw, uncrushed. Three-tenths natural size.





Fig. 5. *Stegodon orientalis*. No. 18630. Palate of adult skull. One-half natural size.





Fig. 6. *Stegodon orientalis*. No. 18640. Palatal view of young skull. One-half natural size.



species must be with *R. unicornis*. At all events, the Yen-ching-kao rhinoceros is a near relative of the typical modern Indian rhinoceros.

The type of *R. sinensis* consists of parts of upper and lower teeth, probably of different individuals. We designate the following as a neotype.

NEOTYPE.—A crushed skull, Amer. Mus. No. 18628.

CHARACTERS.—A large nasal horn. No clear indications of a second horn. Occiput apparently rather posterior in position. Teeth moderately hypsodont, slightly less so than in *R. indicus*. Premolars 130; length of molars, 160;  $p^1$  small, deciduous. Both external ribs prominent on  $p^{2-4}$ , posterior rib weak on  $m^1$ , wholly absent on  $m^{2-3}$ , the anterior rib prominent on all three molars. Crochet prominent on  $p^3-m^3$ , doubled on  $p^4-m^1$ ; crista rudimentary except on  $p^2$ , where it is prominent. No antecrochet save as an obscure swelling. Postfossette on  $p^3-m^1$  only when considerably worn. The two inner cones of  $p^2$  strongly twinned, slight twinning on  $p^{3-4}$ .

The above characters are shown on the neotype and in Owen's type, so far as it goes. A number of incomplete skulls, palates and upper jaws and teeth show more or less variation in the external ribs, details of the crochet, crista and posterior fossette, but in all it may be said that the crochet is strong and more or less reduplicate, the crista and antecrochet weak or absent, the postfossette moderately developed, the external ribs variable, the teeth subhypsodont, premolars considerably smaller than molars, but  $p^2$  unreduced and only  $p^1$  vestigial, molars subequal,  $m^3$  smallest of the three.

The characters of the teeth in the neotype are strongly suggestive of affinity to the Indian and Javan rhinoceroses, combining peculiarities of the two; the referred specimens bring it on the whole nearer to the Indian species. None of our specimens has the premaxilla preserved sufficiently to demonstrate the presence or absence of upper incisors; but the cheek teeth are nearer to the true rhinoceroses than to *Atelodus* and the proportions of the anterior end of the lower jaw agree best with *R. indicus*. The neotype skull is too badly crushed to be decisive as to the characters of the occiput, and no other specimens show this region. The position of the horn, on the nasals but not quite terminal, is like *R. indicus* and unlike *Atelodus*.

In the skeleton, including especially the length and proportions of the limb bones and feet, all the Yen-ching-kao rhinoceros material agrees fairly closely with *R. indicus*.

Among the numerous fossil species described we find certain Indian and western Eurasian forms that may be nearly related, especially *R. platyrhinus*, *palæindicus*, *sivalensis*.

The species described by Koken and Schlosser are founded upon tooth distinctions, of which the constancy is doubtful, to judge from our



collections. Both Schlosser and Matsumoto, in sorting out the material described and assigning it to various species and horizons, have attached great importance to the degree of fossilization and the quality of the matrix. Wide variation is shown in our collections in this respect, from almost unaltered and recent-appearing to thoroughly fossilized teeth and bones in hard clay matrix. But we cannot associate these differences at present with any faunal distinctions and it is probable that they are due chiefly or wholly to the accidents of location of the specimen, whether in the path of mineralizing waters or protected from their action. The present species can be satisfactorily placed as to its relationships, but not as to its nomenclature and synonymy.

**AFFINITIES.**—*R. sinensis* is clearly excluded from *Aceratherium*, *Teleoceras* or *Cælodonta* and apparently from *Opsiceros*. Affinity with *Ceratotherium* is not especially indicated. All the positive evidence goes to show that it is a near relative of the true *Rhinoceros*, but specifically distinct from either the Indian or the Javan species, nearer perhaps to the former.

#### **Tapirus sinensis** Owen

Besides the teeth described by Owen, Koken figured a number of teeth and Schlosser records two from the Haberer collections. The latter were obtained at I-chang, a hundred miles down-river from Yen-ching-kao; Koken's material is said to be mostly from caves in Yun-nan or other southern provinces. They are all referred to the Pleistocene by Schlosser. It would appear that Owen's species is closely related to *T. indicus*, perhaps doubtfully distinct. Our tapir material consists of skulls, jaws, etc., of a very much larger species described below. It is not close to the modern Malayan tapir; whether the genus is distinct remains to be determined. *T. sinensis* is not represented in the Granger collection.

#### **Chalicotherium sinense** Owen

Owen's collection contained one upper molar. Koken described a supposed  $p_4$  ( $m_1$  according to Schlosser). Our collection contains a single lower molar, No. 18453, probably  $m_3$ . It affords no especial light upon the relations to the Indian *C. sivalense*.

#### **Hyæna sinensis** Owen

No. 18392, upper and lower jaws, is referred to this species; also Nos. 18395–7, isolated parts of jaws.



Owen distinguishes the species as larger and more robust than the modern *H. crocuta*, much larger than the Asiatic striped hyæna, and as allied to the African and not to the Asiatic species, "unlike the European cave hyæna."

## NEW GENERA AND SPECIES IN THE YEN-CHING-KAO COLLECTION

### Spalacidæ

#### *Rhizomys troglodytes*, new species

TYPE.—No. 18408, skull and jaws.

PARATYPES.—Nos. 18401–18417, a series of skulls and jaws, some with parts of skeleton associated.

DISTINCTIVE CHARACTERS.—(a) Size large, length of skull incisors to condyles = 77–85 mm.; (b) skull rather long and narrow, postorbital crests contracting sharply behind the orbits to a long and well-marked sagittal crest; (c) infra-orbital foramen sub-triangular, the maxillary crest in front of it and plate beneath extended upward on the side of the muzzle almost to its upper surface; (d) nasals long, narrow, wedge-shaped, tapering backwards almost to a point; (e) squamosals fail to reach the sagittal crest superiorly or the postorbital constriction anteriorly; (f) occiput strongly sloped forward; (g) posterior nares narrow and contracted transversely; (h) bulla somewhat flattened inferiorly, strongly convex anteriorly, culminating in a ridge directly behind the posterior lacerate foramen, slightly reflexed on the anterior inner border against the basisphenoid; (i) carotid foramen lying close behind the basisphenoid-basisoccipital suture and the bulla extending a considerable distance in front of it; (j) bulla strongly reflexed posteriorly upon the surface of the paroccipital process; (k) inferior surface of auditory meatus strongly concave both ways, without any longitudinal ridge, and the opening large and flaring; (l) incisors strongly convex, the points of the upper pair directed somewhat backward, the anterior faces of the lower pair strongly flattened, of the upper pair, moderately so; (m) first upper molar somewhat, and first lower molar considerably reduced and  $m^1$  wearing to a lower grinding plane than the others; (n) third upper molar unreduced, approximately equal to  $m^2$  in size, the posterior portion of the third lower molar correspondingly enlarged and broadened.

Of the above characters, Nos. *c*, *d*, *e*, *f*, *g*, *h*, *i*, *k*, *l*, *m*, and *n* appear to be characteristic of *Rhizomys* proper as against *Nyctocleptes*. Nos. *a* and *j* resemble the latter, while *b* is peculiar. The affinities of the species are thus clearly shown to be with the much smaller *Rhizomys* of China, although in size and one or two characters associated with size it is suggestive of the large Malayan bamboo-rat, *Nyctocleptes sumatrensis*, etc., which it fully equals in size.

The above comparisons were made with modern skulls from South China collected by Mr. Andrews and a series of Malayan skulls in the National Museum loaned through the courtesy of Dr. Gerrit S. Miller and Mr. J. W. Gidley.





Fig. 7. *Rhizomys troglodytes*. Type skull, No. 18408. Natural size.



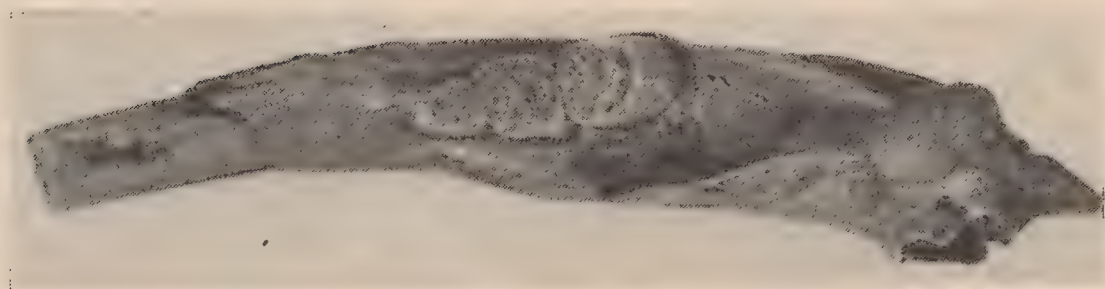


Fig. 8. *Rhizomys troglodytes*. Side view of skull and jaws, No. 18416. Outer and top views of lower jaw, No. 18413. Both natural size.



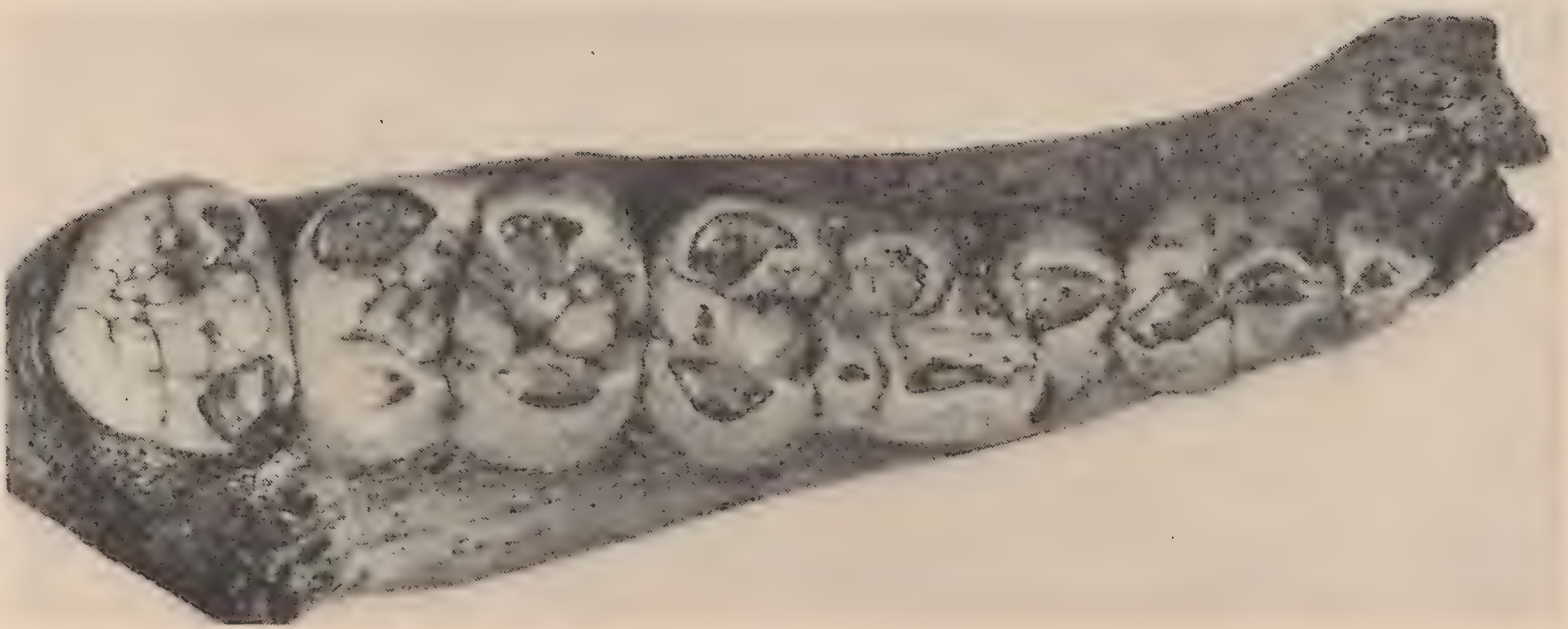


Fig. 9. *Aeluropus fovealis*. No. 18385, type. Lower jaw, outer and crown view of teeth. Natural size.





Fig. 10. *Aeluropus fovealis*. No. 18388. Lower jaw, outer and top views. Natural size.



## Ursidæ

*Æluropus*<sup>1</sup> *fovealis*, new species

TYPE.—No. 18385, right lower jaw with  $p_4$  to  $m_3$ , also left  $m_3$  of the same individual.

DISTINCTIVE CHARACTERS.—The teeth resemble those of *Æ. melanoleucus* as figured by Lankester, 1901, except in the following particulars: the protocone of  $p_4$  is distinctly higher than the anterior and posterior cusps;  $m_1$  retains more of the normal canassial construction, the anterior end being less quadrate, protoconid larger, paraconid more advanced and the whole tooth is relatively larger;  $m_2$  and  $m_3$  are broader, though not longer. Bardenfleth's figure in 1913 of the teeth of a specimen also in the British Museum agrees much more closely in proportions with our specimen and, if both are accurate, would suggest that the differences noted above are individual rather than specific. However, as it seems unlikely that a species of the Carnivora would persist unchanged from the Pliocene to the present day, it appears better to regard the species provisionally as distinct. Three other specimens, Nos. 18386–8, are referred to the species. Two of them show the unworn  $m_1$  in broken lower jaws. The third is a lower jaw with  $m_{1-2}$  complete, so much larger and more robust than the type that we hesitate to include it under the same species.

The affinities of *Æluropus* appear to be with *Hyænarctos*, as has been observed by Lydekker,<sup>2</sup> Winge<sup>3</sup> and other writers. Its systematic position appears to be clearly in the family Ursidæ,<sup>4</sup> although of a distinct subfamily from the true bears. Bardenfleth<sup>5</sup> has presented the evidence for this view very clearly. The occurrence of *Æluropus* almost completely modernized in the Pliocene, if these deposits are in fact Pliocene, contemporary, or nearly so, with *Hyænarctos*, shows that it cannot be a direct descendant, although *Hyænarctos* seems to be in general structurally ancestral.

Lydekker<sup>6</sup> has reported a species of *Hyænarctos* from the collection of Chinese fossils described by Owen. Schlosser<sup>7</sup> gives reasons (not very convincing) for regarding it as Pleistocene and notes an incisor and  $m_3$  in the Haberer collection at Munich, but doubts their pertinence to this genus. They approach the amphicyons, differing from *Hyænarctos* in quite an opposite sense from the present species.

<sup>1</sup>*Æluropus* = *Æluropoda*, for the purists.

<sup>2</sup>Lydekker, R. 1896. 'Geographical History of Mammals,' p. 321.

<sup>3</sup>Winge, H. 1896. 'Jordf. og. nulev. Rovdyr (Carnivora) fra Lagoa Santa,' p. 62. These are probably by no means the earliest authorities, for the comparison is too obvious to have escaped notice. It is at least implied in Flower's arrangement of the genera in the 'Catalogue of Mammals, Mus. Roy. Coll. Surgeons.'

<sup>4</sup>As placed by most authors. Osborn in the 'Age of Mammals,' following Lankester's authority, places it in the Procyonidæ.

<sup>5</sup>Bardenfleth, K. S. 1913. 'On the Systematic Position of *Æluropus melanoleucus*.' Mindesk. f. Japetas Steenstrup, Kobenhavn.

<sup>6</sup>Lydekker, R. 1885. 'Cat. Foss. Mam. Brit. Mus.,' Part I, p. 157, fig. 23.

<sup>7</sup>Schlosser, M. 1903. 'Fossile Säugethiere Chinas,' p. 23.





Fig. 11. *Ursus kokeni*. No. 18384, type. Lower jaw, outer and top views. Natural size.

### ***Ursus kokeni*, new species**

TYPE.—No. 18384, a lower jaw with  $m_{1-2}$  and adjacent alveoli.

DISTINCTIVE CHARACTERS.—Jaw very short and deep as in the sun-bear *U. malayanus*, but size large, comparable with *U. arctos*;  $m_1$  narrow and long, lacking the metastylid cusp of *U. malayanus*;  $m_2$  rather short and wide, wider posteriorly than anteriorly.

It is very likely that the molar figured by Koken as *U. aff. japonicus* is of this species.

### ***Arctonyx rostratus*, new species**

TYPE.—No. 18393, skull lacking the zygomatic arches and with damaged teeth.

PARATYPES.—Nos. 18394, skull, and 18382, 18383, lower jaws.

DISTINCTIVE CHARACTERS.—Length of skull, premaxillæ to condyles, 148 mm.; sagittal crest narrow, distinct;  $p_1^1$  absent,  $p_2^2$  larger than in *A. collaris* and more clearly two-rooted, the diastema behind  $p^2$  greater than length of  $p^3$ ;  $p^4$  larger with inner cusp better developed and more antero-internal;  $m^1$  larger, broader and more quadrate in form; auditory meatus and posttympanic process broad, massive and





Fig. 12. *Arctonyx rostratus*. No. 18393. Type skull, top view. Natural size.





Fig. 13. *Arctonyx rostratus*. Type skull, No. 18393, palatal view. Natural size.





Fig. 14. *Arctonyx rostratus*. No. 18381. Lower jaw, outer and top views. Natural size.

flattened, occiput broader at the base.  $P_3$  and  $p_4$  are more robust than in *A. collaris* and there is no diastema between them;  $m_1$  and  $m_2$  are considerably larger and more robust, with the cusps more conical in form.

This species differs but little from Milne Edwards' drawing of *A. collaris*. The differences from a specimen obtained in the mountains of Shensi (with which the above comparisons are made) are more considerable but may also be reduced in essence to the greater size and robustness of the fossil species and the somewhat higher degree of specialization of its modern relative.

The construction of the teeth in *Arctonyx* is essentially the same as in *Meles*, to which it is rather nearly related, in spite of the wide difference in proportions.



***Cyon antiquus*, new species**

TYPE.—No. 18389, a pair of lower jaws. No. 18583, parts of crania, limb bones and vertebræ of a canid of appropriate size and characters are provisionally referred to the species.

DISTINCTIVE CHARACTERS.—Metaconid distinct upon  $m_1$  and  $m_2$ . Teeth slightly more robust than in our specimens of *C. alpinus*, more decidedly larger and heavier than in *C. javanicus*.

There is some question as to the validity of this species, as Mivart in his 'Monograph of the Canidæ' figures the metaconid as present on  $m_1$  of both species of *Cyon*, although it is absent in our specimens referred to them. It may therefore be a variable character.

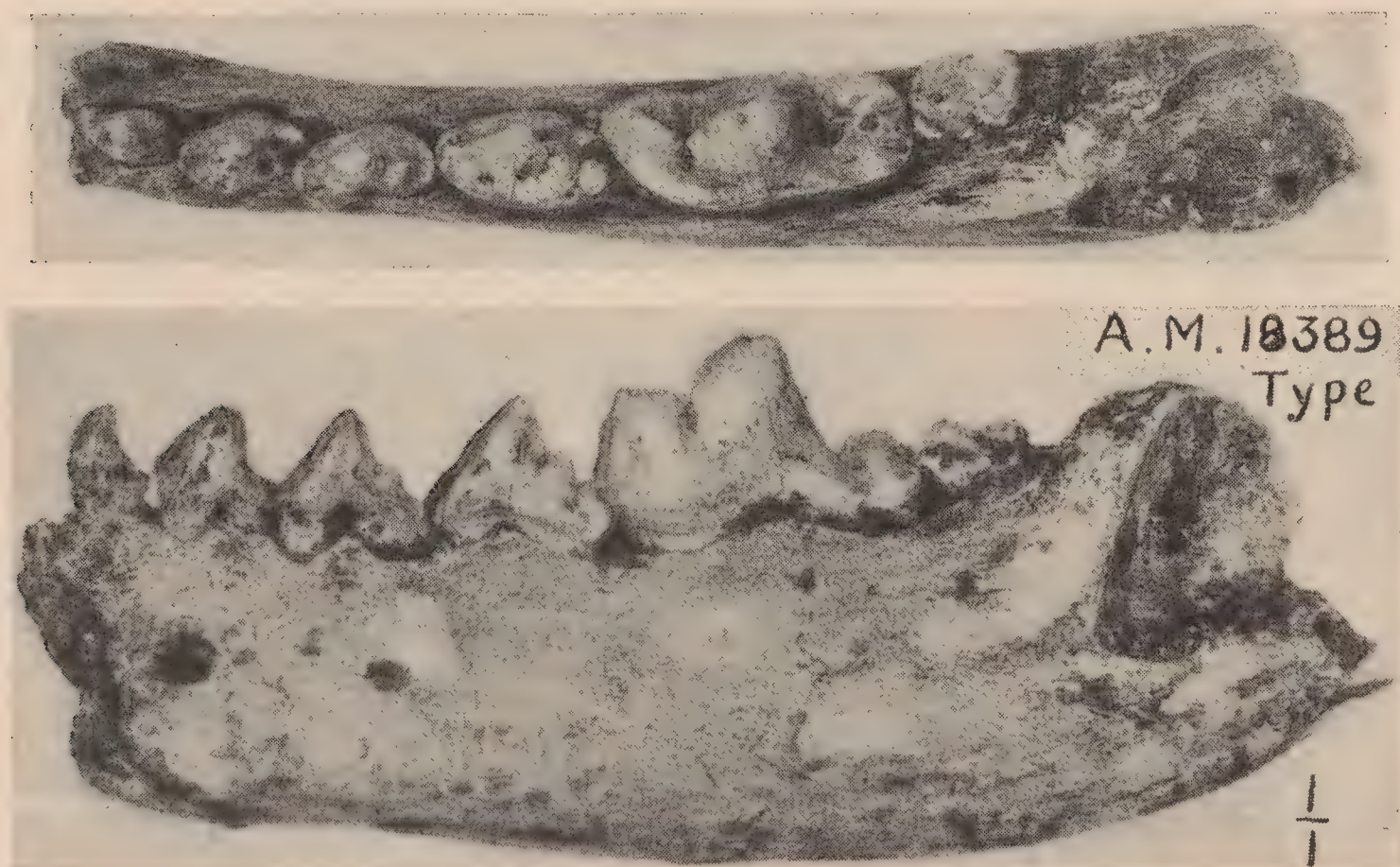


Fig. 15. *Cyon antiquus*. Lower jaw, No. 18389, type specimen, top and outer views. Natural size.

***Felis* aff. *tigris* Linnæus**

No. 18624, a complete skull and jaws; also a part of skull with lower jaws associated, and a number of jaws and limb bones more or less associated, are referred here. In comparison with a series of skulls of the modern tiger we have been unable to recognize any constant distinctions for the fossil form, and therefore refer it to *F. tigris*, although a more minute and exhaustive comparison might very well show valid specific distinctions.

There is no doubt, at any rate, that it belongs nearer to the tiger than to the lion and that it is quite distinct from *F. cristata* of the Siwalik Pliocene.





Fig. 16. *Felis* aff. *tigris*. No. 18624, skull and jaws. One-half natural size.



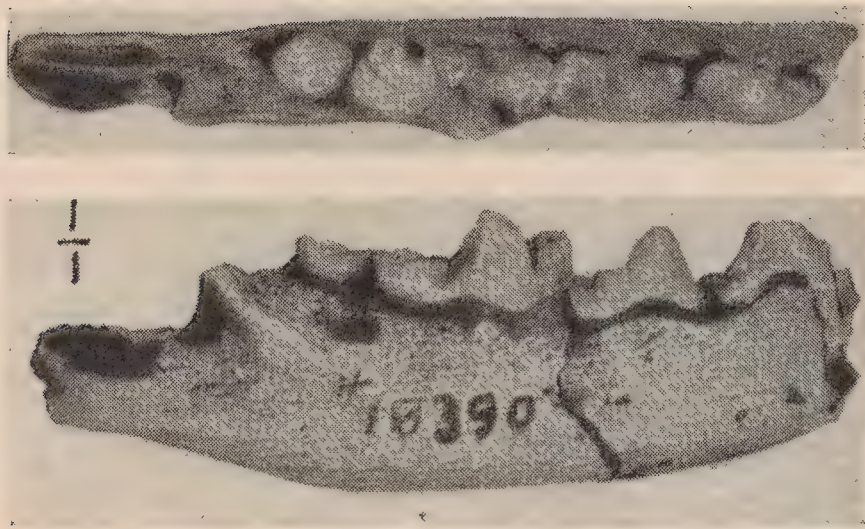


Fig. 17. *Viverra* sp. Lower jaw, No. 18390, top and outer views. Natural size.

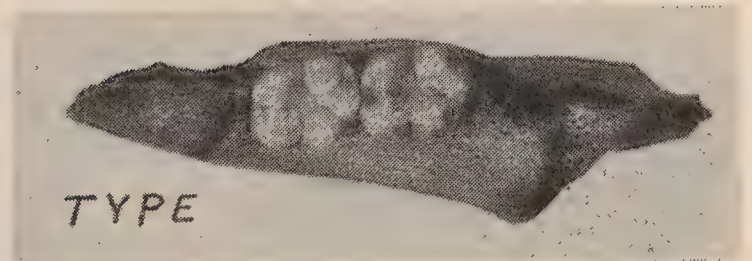


Fig. 18. *Bunopithecus sericus*. No. 18534, type, lower jaw fragment, top and outer views. Natural size.



Fig. 19. *Rhinopithecus tingianus*. No. 18466. Type skull, side view. Natural size.



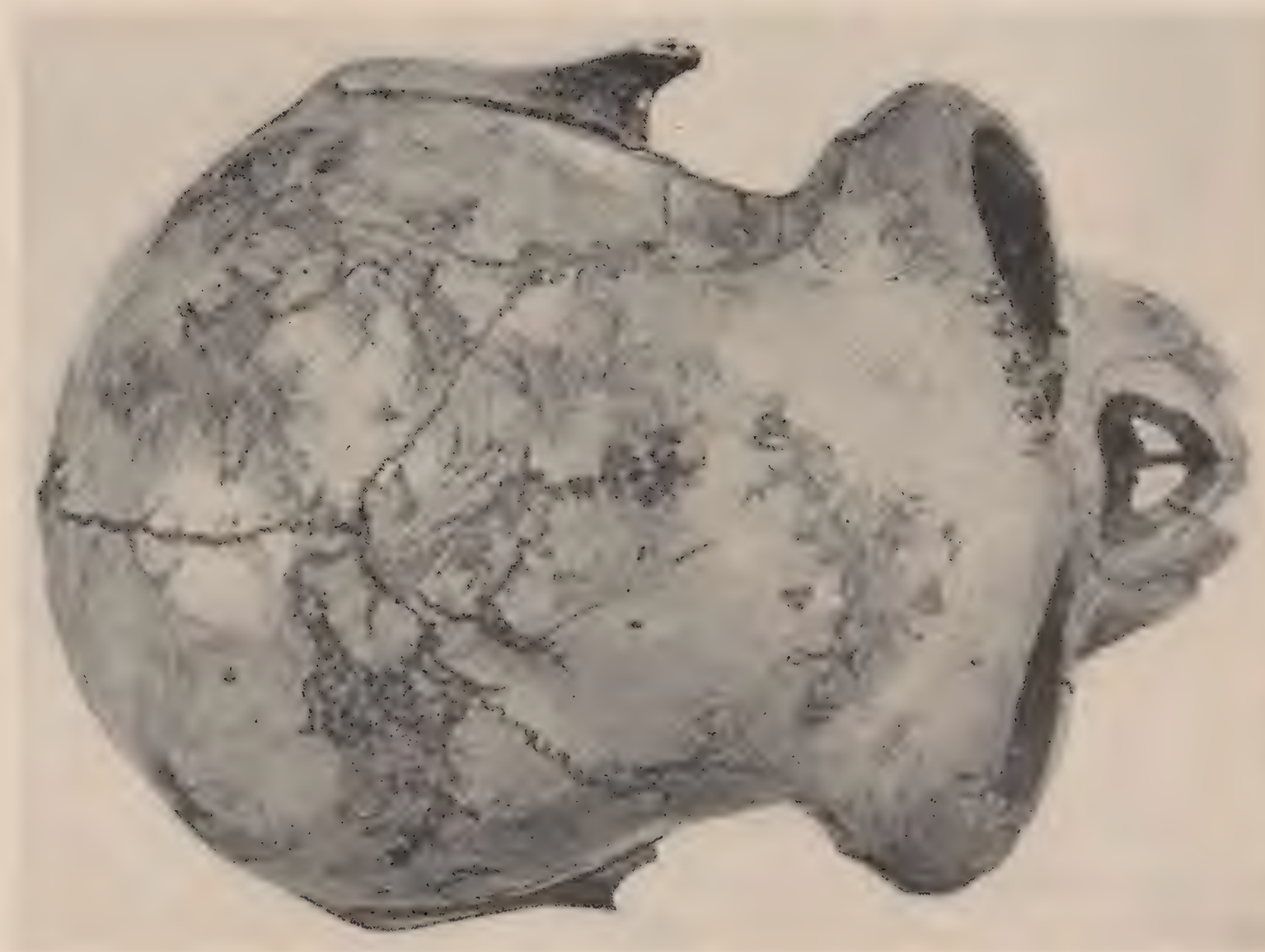


Fig. 20. *Rhinopithecus tingianus*. No. 18466. Type skull, top and palatal views. Natural size.



**Bunopithecus sericus**, new genus and species

TYPE.—No. 18534, a lower jaw with  $m_{2-3}$  on the left side.

GENERIC DISTINCTIONS.—Jaw and teeth much as in *Hylobates* except for greater width of molar and large size of hypoconulid on  $m_2$  and  $m_3$ .

The heels are slightly broader than the anterior half of the teeth and the hypoconulid is as large as the entoconid on both teeth. In the gibbon it is small on  $m_2$  and absent on  $m_3$ ;  $m_3$  is narrower and smaller than  $m_2$  in the gibbon but broader in *Bunopithecus*.

The species is about the size of the hoolock.

**Rhinopithecus tingianus**, new species

TYPE.—No. 18466, a skull, immature, retaining the milk premolars, and the last molar not yet emerged.

PARATYPES.—Nos. 18467–9, upper and lower jaws.

DISTINCTIVE CHARACTERS.—Larger and more robust throughout than *R. roxellanae*. Size about as in *R. bieti* but with much smaller teeth.

The modern langhur monkeys of this genus have a somewhat ill-defined range in northwestern and southwestern China and eastern Thibet. This species is typical of the genus, not in any marked degree primitive or synthetic in generic position. It is named in honor of Dr. V. K. Ting, the able and progressive director of the Geological Survey of China.

**Tapirus (Megatapirus) augustus**, new species

TYPE.—No. 18433, skull and jaws.

PARATYPES.—Nos. 18428, 18431, and 18432, skulls, the latter two with lower jaws.

DISTINCTIVE CHARACTERS.—Teeth and skull about one-fourth larger lineally than *T. indicus* or *terrestris* and almost as much exceeding *T. sinensis* in size. Anterior premolars more molariform than in *T. indicus*, the inner cusp and cingulum much more developed, especially in  $p^1$  which in *T. augustus* is wider than long (?). Skull very short and deep, the vomer higher and thicker than in *T. indicus*, much more so than in *T. terrestris*.

This species far exceeds in size any living tapir of which we can find record and differs so considerably in proportions of skull and details of tooth construction that we consider it provisionally as representing a distinct subgenus. All of our tapir specimens appear to be referable to this gigantic species. *T. sinensis* is not present here, although the specimens provisionally referred to it by Schlosser may be *T. augustus*. Although resembling *T. terrestris* in the relative complexity of the anterior premolars, it appears in the skull to be an exaggerated type of *T. indicus*, deeper and shorter with more massive vomer, high-set nasals, etc.





Fig. 21. *Tapirus* (*Megatapirus*) *augustus*. No. 18433, type skull, side view. Two-fifths natural size.





Fig. 22. *Tapirus augustus*. No. 18433. Palatal view of type skull. Two-fifths natural size.





Type

A.M. 18433

$\frac{2}{5}$

Fig. 23. *Tapirus augustus*. No. 18433. Lower jaw of type, top view. Two-fifths natural size.





Fig. 24. *Tapirus augustus*. No. 18433. Lower jaw of type, outside view. Two-fifths natural size.



MEASUREMENTS

|                                             | No. 18433 | No. 18428 | No. 18432 | <i>T. sinensis</i> | <i>T. hayssi</i><br>Phila. Acad. | <i>T. malayanus</i><br>A. M. 14106 | <i>T. americanus</i><br>A. M. 36198 |
|---------------------------------------------|-----------|-----------|-----------|--------------------|----------------------------------|------------------------------------|-------------------------------------|
| Skull length pmx-condyles                   | E. 530    | E. 530    |           |                    |                                  | 417                                | 390                                 |
| “ width                                     | E. 280    |           |           |                    |                                  |                                    |                                     |
| Upper teeth, p <sup>1</sup> -m <sup>3</sup> | 214       | 212       | 205       |                    | 174                              | E. 151                             | 145                                 |
| “ molars m <sup>1-3</sup>                   | 101       | 103       | 101       |                    | 79                               |                                    | 70                                  |
| Diameters of p <sup>1</sup> a-p×tr.         | 27×25     | 26×23     |           |                    | 20×19                            | 18×14                              | 17×17                               |
| “ “ p <sup>2</sup>                          | 27×31     | 27×33     | 28×34     |                    | 21×25                            | 20×23                              | 18×22                               |
| “ “ p <sup>3</sup>                          | 30×36     | 29×38     | 29×37     | 25×31              | 21×25                            | 23×27                              | 19×25                               |
| “ “ p <sup>4</sup>                          | 29×38     | 29×39     | 30×38     |                    | 22×26                            |                                    | 19×27                               |
| “ “ m <sup>1</sup>                          | 31×38     | 31×40     | 31×37     |                    | 24×28                            | 24×25                              | 19×24                               |
| “ “ m <sup>2</sup>                          | 36×40     | 35×43     | 34×40     | 29×31              | 26×30                            | 27×30                              | 24×26                               |
| “ “ m <sup>3</sup>                          | 34×40     | 34×38     | 34×40     | 27×31 <sup>1</sup> | 26×30                            |                                    | 25×26                               |
| Lower teeth p <sub>2</sub> -m <sub>3</sub>  |           |           | 199       |                    | 161                              | 152                                | 136                                 |
| “ molars m <sub>1-3</sub>                   | 104       |           | 107       |                    | 89                               |                                    | 70                                  |
| Diameters of p <sub>2</sub>                 | 20×22     |           | 34×19     |                    | 25×17                            | 24×13                              | 20×15                               |
| “ “ p <sub>3</sub>                          |           |           | 31×24     | 26×19              | 22×19                            | 24×19                              | 20×19                               |
| “ “ p <sub>4</sub>                          | 31×25     |           | 31×26     |                    | 23×19                            | 25×17                              | 21×19                               |
| “ “ m <sub>1</sub>                          | 32×24     |           | 32×25     | 27×21              | 27×19                            | 24×18                              | 21×17                               |
| “ “ m <sub>2</sub>                          | 34×27     |           | 35×26     | 29×21              | 28×21                            | 28×21                              | 25×19                               |
|                                             | 38×28     |           | 38×27     |                    | 28×21                            |                                    | 26×19                               |

<sup>1</sup>From Owen's figures.





Fig. 25. *Sus* sp. cf. *hyotherioides* Schl. No. 18445, skull and jaws. One-third natural size.

***Sus* compare *S. hyotherioides* Schlosser**

This is a species about the size of the modern *Potamochoerus* but  $p^4$  is larger and more complex.

***Proboselaphus watasei* Matsumoto**

Several incomplete skulls, numerous jaws and skeletal bones are provisionally referred to this species. If the reference be correct, it would appear to be rather nearly related to the nilghai (*Boselaphus*) of India.

***Bibos geron* Matsumoto**

This species was based upon parts of upper and lower jaw. We refer to it a series of skulls, skeletons, upper and lower jaws, etc., of which No. 18465, a fairly complete skull, is selected as neotype. The affinity to the gaur and other species of this group is shown especially in the character of the horns, flattened, angulate, arising from the vertex of the skull and sweeping downward and upward, but not backward.

Koken and Matsumoto record *Buffelus* and *Bison* upon the evidence of teeth. While there is a very large series of Bovinæ skulls, jaws, etc., and a considerable variation in the characters of the teeth, we have not seen among the skulls and horns any evidence of any other true bovine type than *Bibos*. Whether the supposed distinctions among the teeth





Fig. 26. *Bibos ? geron* Matsumoto. No. 18465, skull, top and side views. One-sixth natural size.





Fig. 27. *Bibos ? geron*. No. 18465, palatal view of skull. One-sixth natural size.

are really constant characteristics of the several genera of Bovinæ remains to be verified by more careful comparative study of the materials.

It is quite clear, however, that there are two distinct types of Bovinæ represented in the foot material; one with extremely short metapodials, the other of larger size and with metapodials somewhat longer than in the American bison.

#### AFFINITIES OF THE YEN-CHING-KAO FAUNA

The following faunal list is a preliminary one and may be considerably modified and better defined by further study. It will serve, however, to show the general character of the fauna.



## PRIMATES

|                                |                        |          |
|--------------------------------|------------------------|----------|
| <i>Bunopithecus sericus</i>    | cf. <i>Hylobates</i>   | Malaysia |
| <i>Rhinopithecus tingianus</i> | " <i>Rhinopithecus</i> | W. China |

## FERÆ

|                                 |                           |                  |
|---------------------------------|---------------------------|------------------|
| <i>Ursus kokeni</i>             | " <i>U. malayanus</i>     | Malaysia         |
| <i>Æluropus fovealis</i>        | " <i>Æ. melanoleucus</i>  | W. China, Thibet |
| <i>Arctonyx rostratus</i>       | " <i>A. collaris</i>      | " "              |
| <i>Cyon antiquus</i>            | " <i>C. alpinus</i>       | " "              |
| <i>Viverra</i> sp.              | " <i>Viverra</i> sp. div. | " "              |
| <i>Hyæna sinensis</i>           | " <i>H. crocuta</i>       | Africa           |
| <i>Felis</i> aff. <i>tigris</i> | " <i>F. tigris</i>        | India, E. Asia   |

## GLIRES

|                             |                      |             |
|-----------------------------|----------------------|-------------|
| <i>Rhizomys troglodytes</i> | " <i>R. sinensis</i> | S.-W. China |
| <i>Lepus</i> sp.            |                      |             |

## PROBOSCIDEA

|                            |                  |       |
|----------------------------|------------------|-------|
| <i>Stegodon orientalis</i> | " <i>Elephas</i> | India |
|----------------------------|------------------|-------|

## PERISSODACTYLA

|                               |                     |                            |
|-------------------------------|---------------------|----------------------------|
| <i>Tapirus augustus</i>       | " <i>Tapirus</i>    | Malaysia, tropical America |
| <i>Chalicotherium sinense</i> |                     |                            |
| <i>Rhinoceros sinensis</i>    | " <i>R. indicus</i> | India                      |

## ARTIODACTYLA

|                                         |                           |                  |
|-----------------------------------------|---------------------------|------------------|
| <i>Bibos geron</i>                      | " <i>B. gaurus</i>        | India            |
| ? <i>Bos</i> (cf. <i>grunniens</i> )    | " <i>B. grunniens</i>     | W. China, Thibet |
| ? <i>Antilope</i>                       |                           |                  |
| ? <i>Proboselaphus watasei</i>          | " <i>B. nilghai</i>       | India            |
| <i>Gazella</i>                          | " <i>G. gutturosa</i>     | Thibet           |
| <i>Cervus</i> sp.                       | " <i>C. wapiti</i> , etc. | Central Asia     |
| <i>Sus</i> sp. cf. <i>hyotherioides</i> | " <i>Sus</i> sp. div.     | Malaysia         |

The above list is remarkable, as a cave or fissure fauna, for the scarcity of rodents (other than *Rhizomys*) and small carnivora. While the remains of large animals are abundant and varied, the bamboo-rat is the only rodent, except for a single hare jaw, and no small mustelids or viverrids appear.<sup>1</sup> It is no less remarkable that no trace of Equidæ is found in it, nor of camels, giraffes, typical Canidæ or machærodonts. This, coupled with the abundance of tapirs and deer, may point to a heavily forested condition. The abundance of *Stegodon* and entire absence of *Elephas* and the presence of *Chalicotherium* are the only observed indications of Pliocene age; for the most part the fauna appears to be quite closely related to modern species and might well be considered Pleistocene. The faunal affinities appear to be principally Chinese, partly Malayan, not much Indian; there is nothing especially suggestive of North American or of Siberian affinity. A more careful comparison

<sup>1</sup>In his second season (1922-3) Mr. Granger reports finding good material of small carnivora.—W. D. M.



and identification of the whole fauna, especially of the smaller ruminants, might show a clearer differentiation from the modern species than we have observed in this preliminary study, but could hardly alter materially the geographic and environmental affinities of the fauna. It is such a fauna as one might expect to find in the valleys of southwestern China at any time before the appearance of civilized man, and under climatic conditions similar to those now prevalent. The effect of the clearing and cultivation of the valleys and the lower slopes of the hills by man has been, broadly speaking, to drive the smaller animals to the mountains and to exterminate the larger ones. Some of the extinct types have left relatives, more or less distant, in the jungles of southeastern Asia, more resistant to human encroachment than the Chinese hills. But the tapir, rhinoceros, gaur and *Stegodon* of the Yen-ching-kao fauna, although their nearest existing relatives are of tropical habitat, do not necessarily indicate a warmer Pliocene climate in China. They may quite well have been species adapted to a temperate climate, such as is more definitely indicated by the geographic affinities of the remainder of the fauna.



## Article XVIII.—THE PROBLEM OF THE UINTATHERIUM MOLARS

BY HORACE ELMER WOOD, 2d

The question of the homologies and derivation of the uintathere upper molars presents a difficult problem. My attention was directed to it by Doctor W. K. Gregory, who has also given me in generous measure the benefit of his criticism and suggestions. The drawings are the work of Miss Marcelle Roigneau.

Osborn (1898, 1907) tentatively accepted the view first advanced by Cope (1884) that the upper uintathere molars developed from the *Coryphodon* type as follows (see Figs. 1, 2, 3): "The ectolph swung around so as to form with the protolph a V opening outwards. Just internal to the apex of the V the hypocone is often developed." He says further (1907): "The lower molars of *Uintatherium* are closely linked with those of *Coryphodon* and *Pantolambda* through the genus *Bathyopsis*, which is strictly intermediate in its mandible and inferior molars and thus supports the view that the upper molars also of *Uintatherium* have passed through stages represented in a general way by *Pantolambda* and *Coryphodon*. The steps in this evolution are the most complicated and difficult to understand, especially the rotation of the ectoloph, a feature which is less positively demonstrated than the other features of this exceptional evolution." Finally, he says (1913): "The specimen (i.e., *Bathyopsis*) thus throws no light upon the still unsettled question of the derivation of the uintathere molar from the primitive amblypod type. . . . As a whole the skull and dentition are so closely related to the *females* of the primitive species of *Uintatherium* as to fall almost within the same generic definition. The skull, however, is that of a robust *male*, with well-developed canine tusks, and is consequently to be regarded as in a typical ancestral stage."

Gregory (1910) accepted the "ectoloph rotation hypothesis," "*fide* Osborn." This has become the traditional view, although Scott (1913) enters a slight demurrer when he refers to the Pantodonta as "not ancestral to them (Dinocerata), but collaterally related and descended from a common ancestry." The context and page 285 show that Scott regards *Pantolambda* as probably the common ancestor of the coryphodons and uintatheres.

Although the anterior half of the upper molars of the uintatheres resembles that of *Coryphodon* strikingly, the posterior half is utterly



different. On the other hand, there is a striking uniformity throughout the uintathere premolars and molars, both upper and lower, and the rotation of the ectoloph, as Osborn admitted, is so difficult to understand that it seems worth while to review the whole question of the homologies of the upper cheek teeth of the Uintatheriidae.

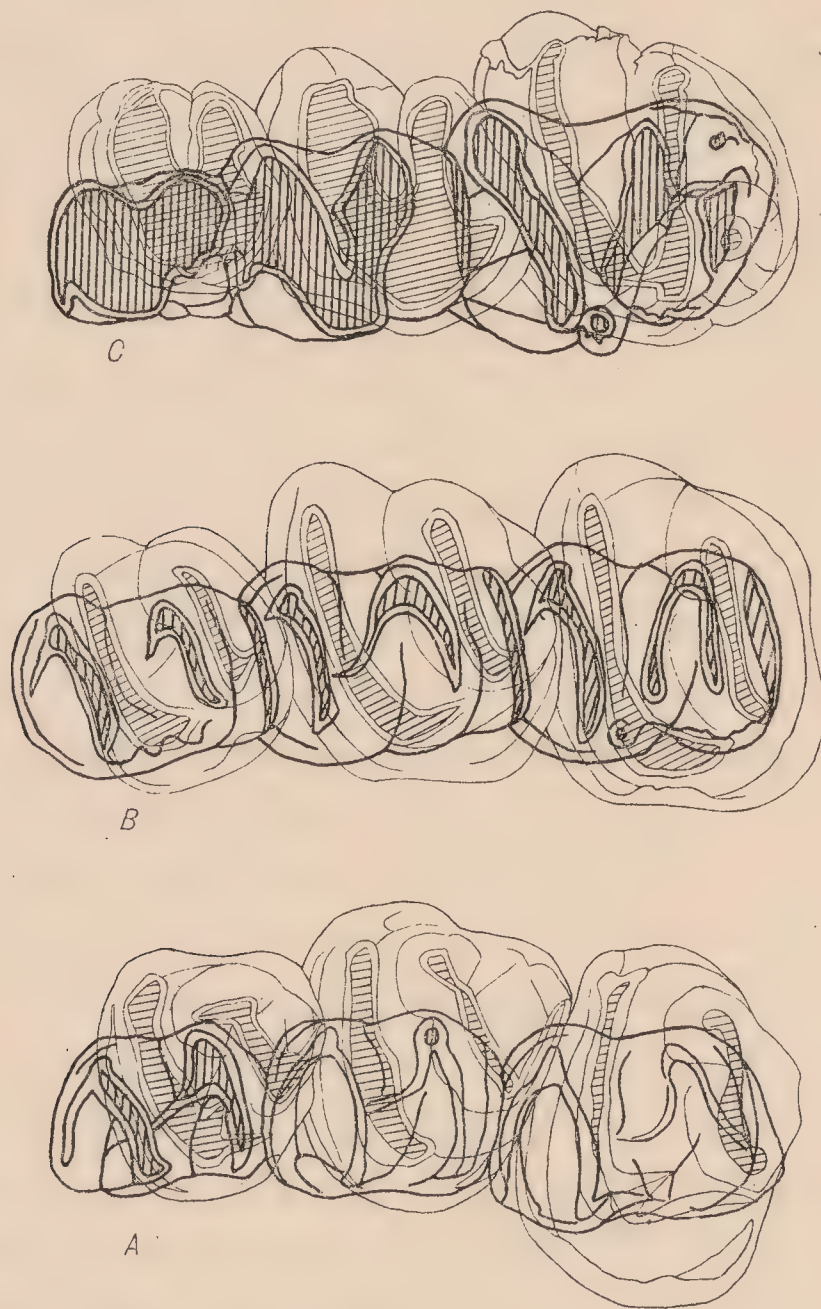


Fig. 1. Occlusal relations of the molars in: a, *Coryphodon testis*; b, hypothetical intermediate form (after W.K. Gregory); c, *Uintatherium stenops*.  $\times \frac{1}{2}$ .

There are a number of objections to the "ectoloph rotation hypothesis." Osborn, with more complete material, apparently withdrew his earlier suggestion that *Bathyopsis* was intermediate between *Coryphodon* and *Uintatherium* (see above). In any case, the lower molars are far more like *Uintatherium* than *Coryphodon*. They are merely a fraction of a stage nearer than *Uintatherium* to the primitive ungulate type represented by *Coryphodon* or *Homogalax* (*Systemodon*).

I feel that too high a value has been placed upon the resemblance between the lower molars of *Coryphodon* and *Uintatherium* (see Figs. 2, 3). If lower molars alone are considered, *Homogalax* is perhaps as good



an ancestor for *Uintatherium* as is *Coryphodon*. In other words, the lower molars of *Coryphodon* and *Homogalax* are equally more primitive than those of *Uintatherium*. An inference of true genetic connection must be founded on stronger evidence than this alone.

The upper molars, always more progressive, must furnish the decisive evidence. The rotation of the ectoloph postulates a surprising fluidity of the ectoloph, associated with virtual immobility of the lower

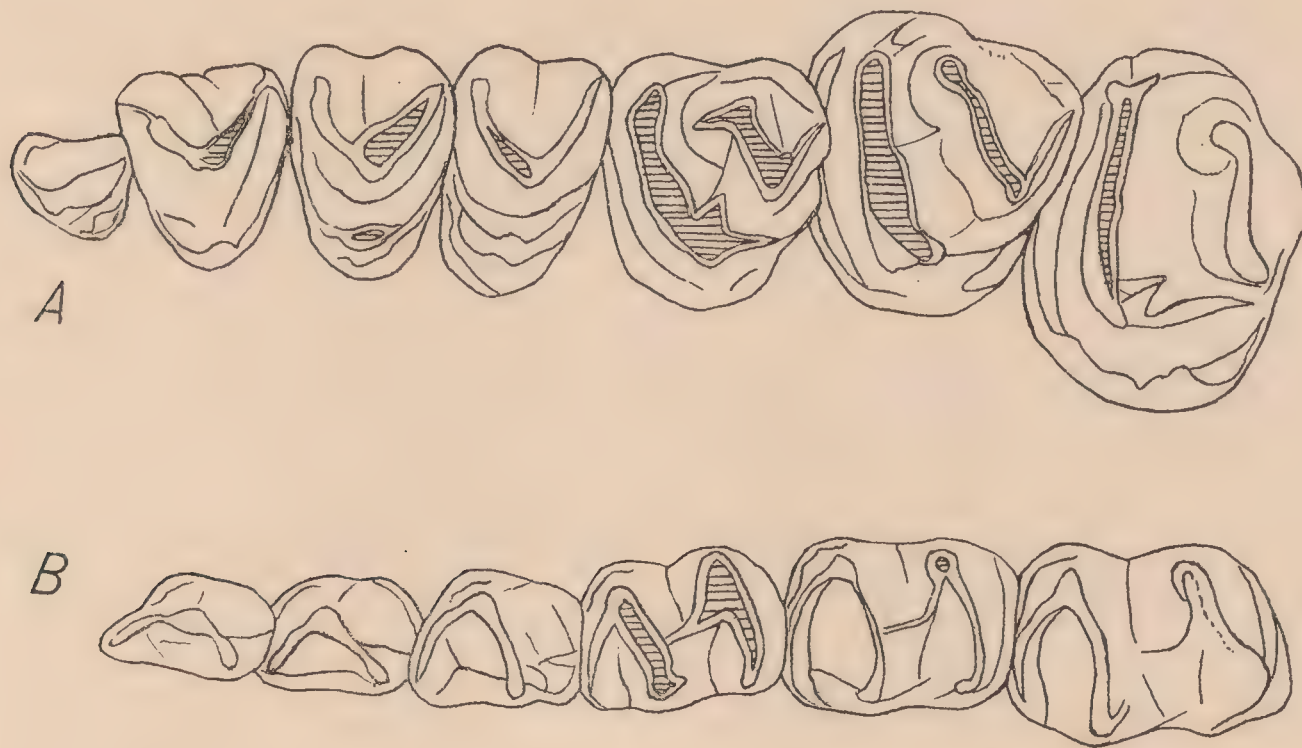


Fig. 2. *Coryphodon testis*: *a*, left upper and *b*, right lower, cheek teeth. After Osborn.  $\times \frac{1}{2}$ .

molars, of the protoloph and of the hypocene (see above). The cusp which Osborn calls the hypocone (see Fig. 4) can, however, hardly be the hypocone on his theory, unless it split off from the cingulum after the upper uintathere molars had been fully developed in all other respects.

Doctor Matthew contributes a note pointing out that Granger has found an as yet undescribed *Bathyopsis*-like uintathere in the summit of the Paleocene and the base of the Eocene in the Clark Fork Basin of Wyoming.<sup>1</sup> Both molars and premolars, upper and lower, have the uintathere pattern most unmistakably. As *Coryphodon* is not known from the Paleocene, the likelihood that the Uintatheriidæ and Coryphodontidæ are parallel phyla is increased. *Pantolambda* itself is virtually a contemporary of this earliest uintathere.

The possibility of the "ectoloph rotation hypothesis" as far as the occlusal relations go, must be admitted. (See Fig. 1.) Hypertrophy of the hypoconulid in *Coryphodon*, associated with partial atrophy of the

<sup>1</sup>American Museum No. 16984, Clark Fork Formation; No. 16786, ? Clark Fork Formation; Nos. 15860, 16063, 16064, Ralston Formation.



posterior V in the lower molars, might change the upper molars from the *Coryphodon* to the *Uintatherium* type. There are, however, no intermediate stages and such a revolution should not be accepted without strong evidence. The resemblance in the body structure of *Coryphodon* and *Uintatherium* is granted (although numerous differences are also

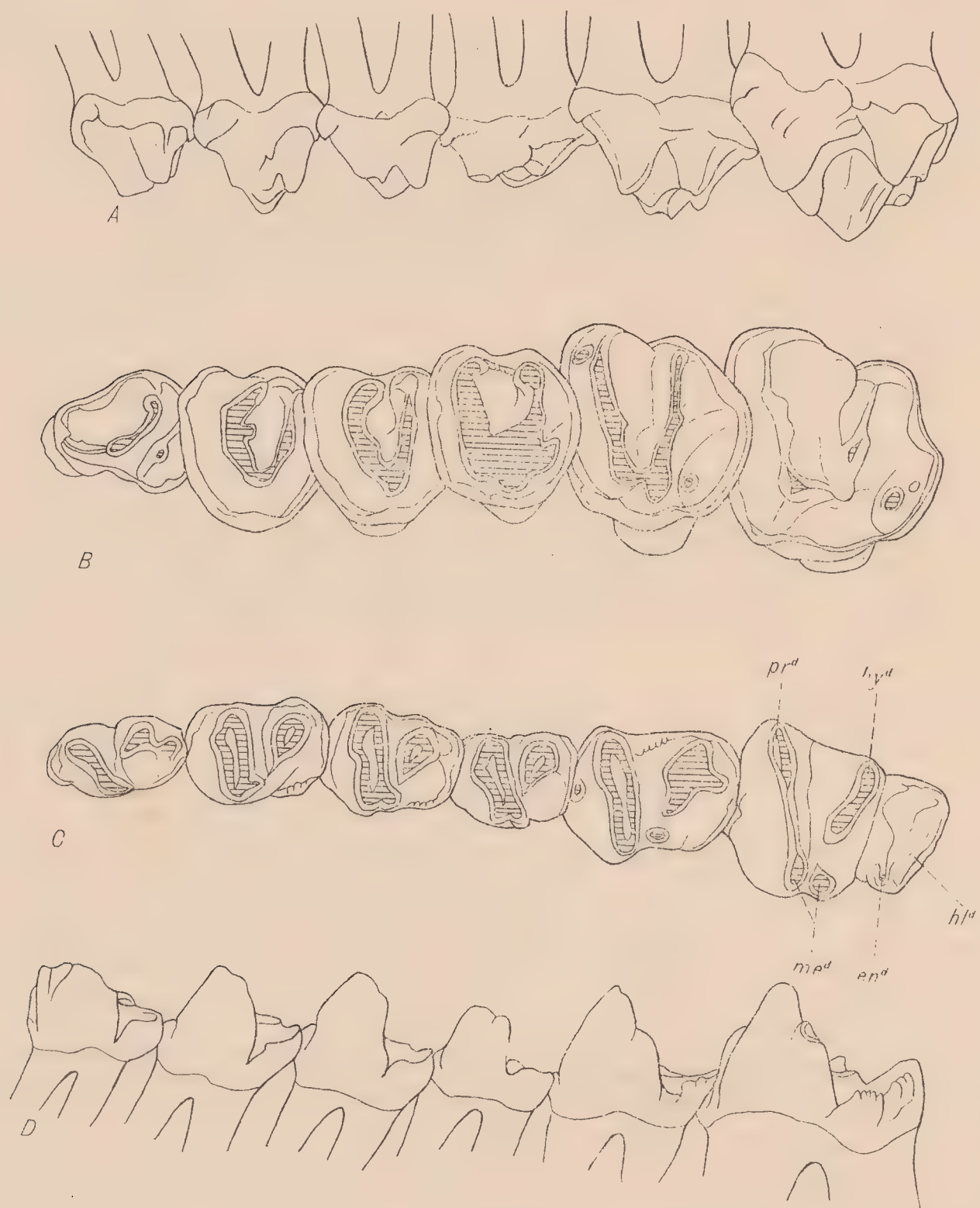


Fig. 3. A, outer, and b, crown views, of the left upper cheek teeth of *Uintatherium lucare*. C, crown, and d, inner, views of right lower cheek teeth of *Uintatherium pugnax*. After Marsh.  $\times \frac{1}{2}$ .

present), but it is no greater than might well occur in two parallel phyla which descended from a common pre-pantolambdid ancestor and acquired giantism independently.

The uintathere lower molars and premolars are strikingly similar to each other in pattern (see Fig. 3). There is, fortunately, entire agree-



ment that the corresponding cusps are truly homologous throughout the lower cheek teeth. Since, however, the lower premolars have become molariform independently of the molars, it suggests the likelihood that the upper premolars, bound up occlusally with the lower premolars and becoming molariform *pari passu*, are now homologous, as well as analogous, with the upper molars. There seems little reason to doubt that the upper premolars are of normal tritubercular pattern, being composed of the "protocone," deutocone and tritocone of Scott's nomenclature. Reversing the reaction  $P^{2-4}-M^{1-3}$ , we reach the tentative conclusion that the V in the upper uintathere molars is (as it seems at first glance), a normal trigon instead of a spurious substitute. The postero-internal cusp of the upper molars fits into this theory as the hypocone, or as a pseudo-hypocone split off from the protocone, and analogous to the tetartocone of premolars. In either case its occlusal relations are absolutely normal.

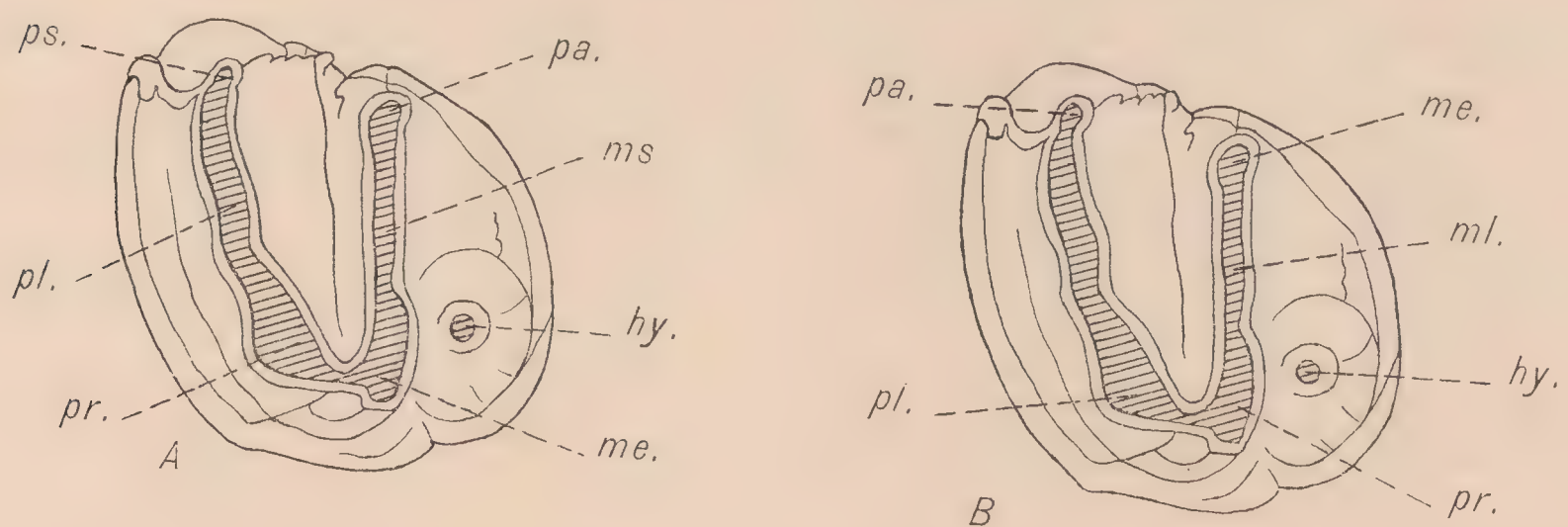


Fig. 4. Third left upper molar of *Uintatherium stenops*. A, Cusps labelled according to Osborn; B, cusps as identified in this paper.  $\times \frac{2}{3}$ .

Although recognizing the deceptiveness of convergence, I feel very strongly the essential unity in ground-plan of the upper cheek teeth. From  $P^2$  to  $M^3$  there are three main cusps, which I believe to be the paracone, metacone and protocone of molars. These cusps form a V of strikingly similar pattern throughout the series. (See Fig. 3.) The parastyle may be traced in all, flattened against the anterior edge of the paracone. The basal cingulum is identical throughout. The lowest point in each V, from  $P^3$  to  $M^3$ , is on the anterior crest of the V, just external to the protocone.

It seems probable therefore that in the Uintatheriidae the trigons and cusps in the molars are homologous with those of the premolars, representing the "secondary trigon" of Gregory (1922). Uintathere molars have a very different pattern from those of *Coryphodon*, formed, accord-



ing to the theory here advanced, from different cusp elements. (See Figs. 1, 4.) This agrees with Scott's view that the Uintatheriidae and Coryphodontidae are parallel but independent phyla. In fact, it separates them somewhat more widely since, if this theory is correct, *Pantolambda*, although an ideal ancestor for *Coryphodon*, is already too highly specialized to give rise to the uintatheres. *Pantolambda* is to the Uintatheriidae as *Palæotherium* is to the Equidae.

The ancestry of the uintatheres is still uncertain.

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# Article XIX.—THE PELVIC MUSCULATURE OF SAURISCHIAN DINOSAURS

BY ALFRED S. ROMER

Von Huene in 1908 first attempted the restoration of the musculature of the pelvic region of the Saurischia. Gregory and Camp ten years later figured the pelvis of *Ornitholestes*, a member of this group, with a tentative localization of the muscular areas of origin. Subsequently, the dinosaurian pelvis was restudied by Dr. W. K. Gregory and a number of illustrations prepared. Through the kindness of Dr. Gregory, I am permitted to publish two of his figures relating to the Saurischia here (Fig. 1). They will be discussed in the body of this paper.

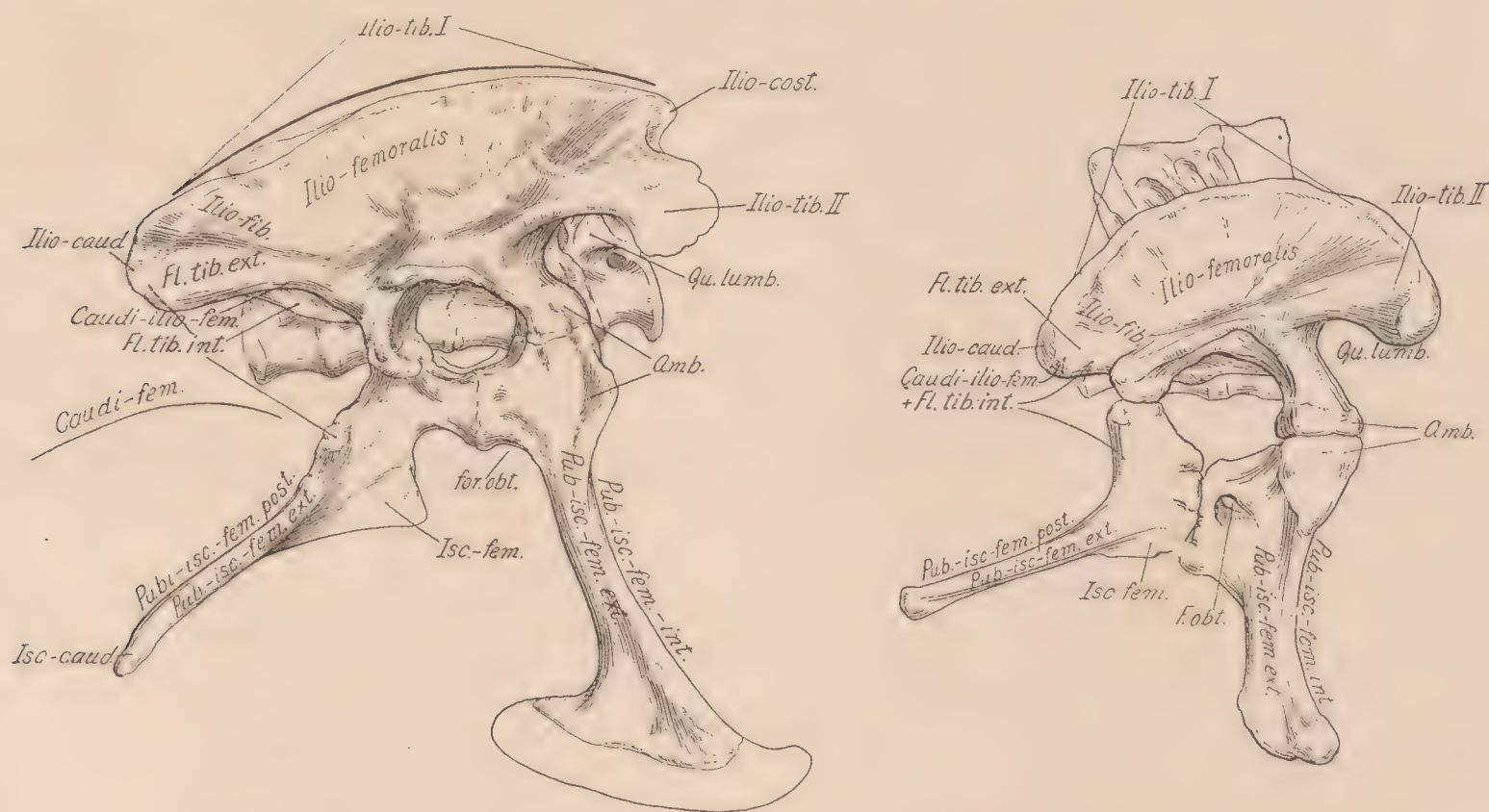


Fig. 1. Previously unpublished restorations of the pelvis in saurischian dinosaurs by Dr. W. K. Gregory. For explanation see text.

Lack of knowledge of the nature of the crocodilian musculature, however, handicapped these attempts to restore the dinosaur pelvis. In order to remove this obstacle the writer has made a study of the pelvic muscles of the Crocodilia, the results of which have recently appeared in this bulletin (1923a). The present paper is an attempt to apply the information gained to the musculature of the Saurischia. The nomenclature adopted in my previous paper will be followed here.

The ilium of the Saurischians presents few major difficulties; I have previously outlined its history (1923). The type of ilium present in the primitive forms from which the "Archosauria" have been derived is represented morphologically by such a reptile as *Dimetrodon* (Fig. 2).



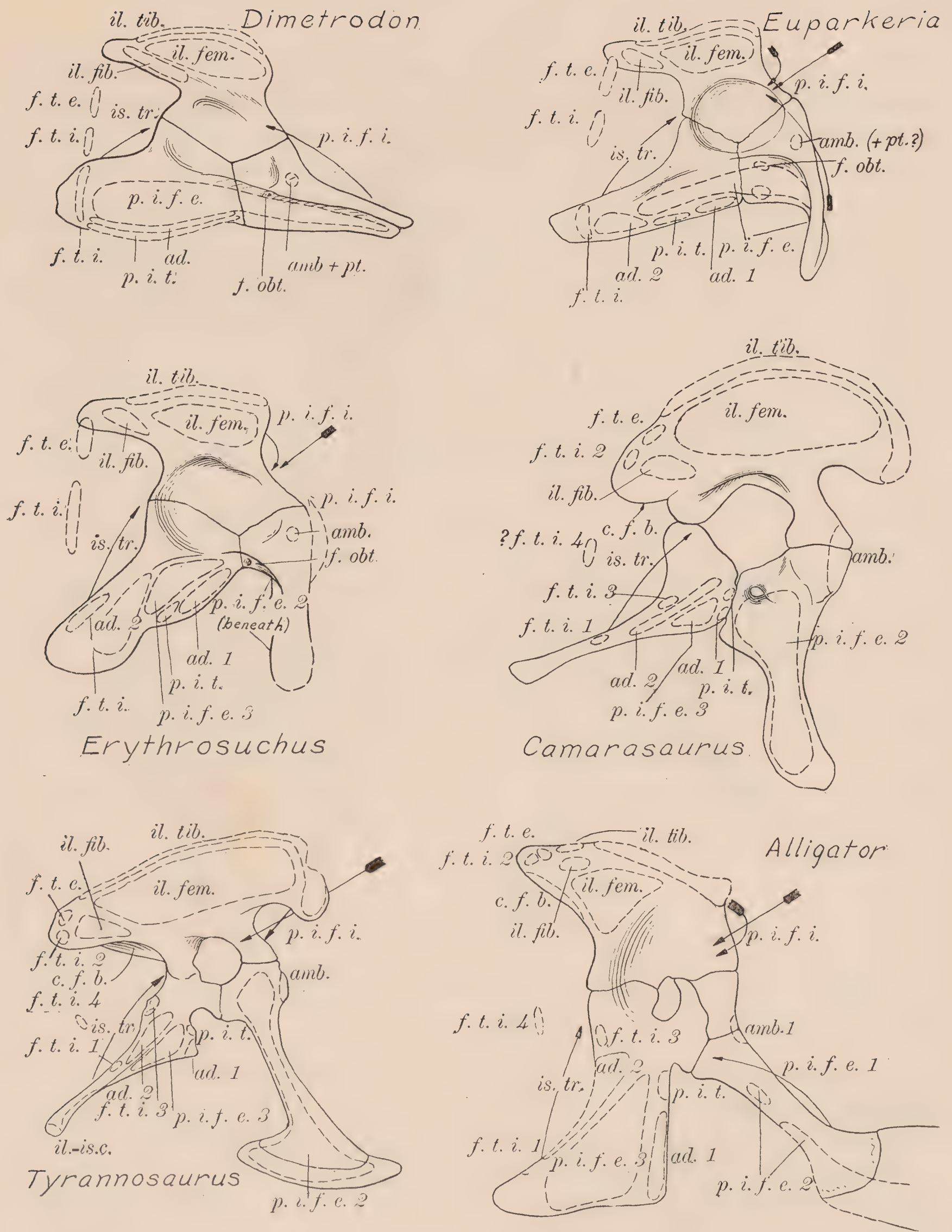


Fig. 2. The musculature of the pelvis in primitive reptiles, the primitive "Archosauria," *Alligator* and saurischian dinosaurs, to show especially the steps in the differentiation of the pubo-ischium.

Abbreviations: *ad.*, adductor; *amb.*, ambiens; *c.f.b.*, coccygeo-femoralis brevis; *c.f.l.*, coccygeo-femoralis longus; *f.obt.*, obturator foramen; *f.t.*, femoro-tibialis; *f.t.e.*, flexor tibialis externus; *f.t.i.*, flexor tibialis internus; *il. fem.*, ilio-femoralis; *il. fib.*, ilio-fibularis; *il.tib.*, ilio-tibialis; *is.tr.*, ischio-trochantericus; *p.i.f.e.*, pubo-ischio-femoralis externus; *p.i.f.i.*, pubo-ischio-femoralis internus; *p.t.*, pubo-tibialis.



It had a broad outer surface extending little, if at all, anterior to the acetabulum. The greater part of this surface was utilized as an area of origin by the ilio-femoralis, while the ilio-tibialis arose tendinously from its dorsal edge. Near the posterior angle was the origin of the ilio-fibularis. The saurischian ilium is comparatively little modified. The external surface is carried forward a short distance without changing the muscular arrangements on its outer surface. This anterior prolongation arches over the pubo-ischio-femoralis internus, a small portion of which arises from the anterior edge of the ilium. Posteriorly, in the Saurischia, portions of the long flexors have gained attachment to the bone, as discussed below. Ventro-posteriorly, the coccygeo-femoralis brevis had an area of origin.

In primitive reptiles (Romer, 1922, p. 578) such as *Dimetrodon*, the pubo-ischium was a solid plate, broken only by the foramen for the obturator nerve, with a continuous ventral symphysis extending in an almost straight line antero-posteriorly. Three principal muscle groups arose from the outer surface of the plate. Externally were the long flexors to the lower leg (pubo-ischio-tibialis, flexor tibialis internus, flexor tibialis externus). Deep to these lay the adductor, running to the distal part of the femur. Still deeper lay the pubo-ischio-femoralis externus, attaching to the proximal part of the femur. That portion of the pubis close to the acetabulum gave origin to the ambiens (a member of the quadriceps group) and to the pubo-tibialis (an anterior member of the long flexor series). Internally the pubis was covered by the pubo-ischio-femoralis internus, which ran up and back to emerge on to the thigh above the ambiens. The ischio-trochantericus took origin from the inner surface of the ischium.

The three chief muscle groups arising from the outer surface of the plate have been greatly modified in the "Archosauria," as known in the Crocodilia and as deduced from the dinosaur pelvis. These changes appear to be correlated with changes in the position of the femur.

In the primitive reptiles, the femur was extended very nearly straight out from the acetabulum in a horizontal direction. The three muscle masses of the plate acted upon it in a plane passing nearly vertically through its long axis, as diagrammatically represented in figure 3.

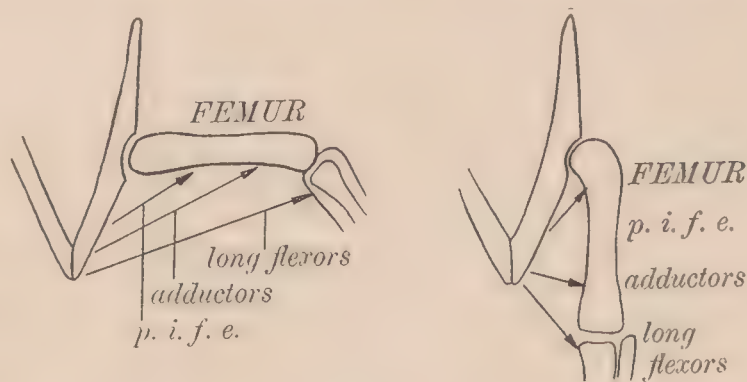


Fig. 3. Diagram to show effects upon the muscles of the pubo-ischium of the change in the femur from the primitive (left) to the archosaurian position (right).



In the "Archosauria," with a higher type of locomotion, the femur (1) has been turned inward anteriorly so as to bring its shaft to a position nearly parallel to the long axis of the body and (2) has, in consequence of the bipedal character of primitive saurischians, been carried downwards and backwards so that, if the primitive plate-like pubo-ischium had been retained, the femur would lie very close to the plate.

The results of such a position on the musculature of the pubo-ischium are obvious from the diagram on the right in figure 3. The long flexors and adductors would be excessively shortened and rendered of little value, especially if situated near the middle of the plate. To correct this, a movement of the areas of origin upwards might be deduced. Further, the main pull of these muscles is now a backward one; a backward migration or a disappearance of anterior portions of these muscles might be expected.

With regard to pubo-ischio-femoralis externus, no movement to a more dorsal position is possible. It is clear, however, that the middle portion of the muscle is at a disadvantage as compared with its anterior and posterior extremities, and the development of anterior and posterior heads of the muscle and the disappearance of the middle portion might perhaps be suggested.

The development of this series of modifications is shown, somewhat diagrammatically, in figure 2. *Dimetrodon* shows the primitive condition; the alligator and sauropod and theropod dinosaurs show the end forms. In the dinosaurs, the muscle areas can be located with almost the same degree of accuracy as in *Alligator*, except that I am unable to locate exactly the origins of pubo-ischio-tibialis and adductor 1 in the theropods. *Euparkeria* and *Erythrosuchus* from the figures of Broom (1906, 1913) are introduced to show the steps by which the changes have taken place, although I am unable to locate exact muscle areas on these forms.

It will be noted that the main change in the form of the pelvis has been a "buckling" of the pubo-ischium, by which the ventral border has been changed from a straight line to an irregular crescent, convex above. Thus the middle part of the pubo-ischium, functionally of the least value, has disappeared.

The apparent "fenestra" caused by this is not at all homologous with the obturator fenestra of other modern reptiles or the obturator foramen of mammals. These openings are essentially a fenestration within the primitive plate, centering about the pubo-ischio-femoralis externus (obturator externus); the line of the symphysis is ventral to the fenestra. In the "Archosauria," on the other hand, the symphysis



turns dorsally as the "buckling" takes place and is continuous in such a form as *Erythrosuchus*; the apparent "fenestra" is ventral to the symphysis. Later, apparently in connection with the strengthening of the sacrum, the primitive symphysis is interrupted and confined to separate pubic and ischiadic surfaces. Hence the ventral edge of the pubis and ischium of the Crocodilia and Saurischia may be considered as the equivalent of the primitive symphysis. Parallels to the obturator fenestra may be sought in excavations in the surface of the ischium in the part of that bone serving as an area of origin for pubo-ischio-femoralis 3 (as in *Ornitholestes*).

If we take a line from the distal end of the ischium to the distal end of the pubis as marking the ventral line of the body, it will be seen that in the saurischian dinosaurs, the muscles of the ischium as a whole are located farther dorsally than in primitive forms or even in the Crocodilia. If the lower half of the saurischian ischium were removed, the remaining triangular area would be almost exactly comparable to the whole of the ischium in the Crocodilia. Such a dorsal movement, as has been noted previously, might be expected in bipedal forms, or those whose ancestors were bipedal.

The pubis of primitive reptiles seems homologous with that of such primitive archosaurians as *Euparkeria* and *Erythrosuchus*. These in turn are similar to the sauropods as regards the pubis; while the theropods have merely carried the reduction farther and eliminated the obturator foramen. In the Crocodilia, further reduction has caused the exclusion of the bone from the acetabulum. But this reduced crocodilian pubis can apparently be carried back through a series showing slight morphological changes to that of the primitive reptiles.

Von Huene (1908) states that the much smaller number of muscles attached to the crocodilian pubis, as compared with that of other living reptiles, tends to show that the crocodilian bone is not the true pubis. But the reasons for a reduction in muscle on the pubis are apparent. In typical reptiles six appendicular muscles may take origin from the pubis: pubo-ischio-femoralis internus, pubo-ischio-femoralis externus, ambiens, pubo-tibialis, adductor and pubo-ischio-tibialis. Of these, the pubo-ischio-femoralis internus has shifted dorsally, as I have explained elsewhere (1923, 1923a), the pubo-tibialis has been lost, and the adductor and pubo-ischio-tibialis have shifted (as expected) posteriorly. This leaves the ambiens and pubo-ischio-femoralis externus as the only possible muscles which might be expected on the pubis in the Crocodilia; and it is these two muscles which are found on the bone commonly called by that name.



The rearrangement of the musculature may now be considered in detail.

The long flexors, as I have termed them, consist essentially of two sets in a primitive reptile. (1) An outer group, made of pubo-ischio-tibialis, from the ventral edge of the pubo-ischium, and a portion or portions of the flexor tibialis internus originating from the region near the posterior ventral angle of the ischium or the lower end of the ilio-ischiadic ligament. (2) An inner group, consisting of pubo-tibialis, from the pubis near the acetabulum, of a portion of flexor tibialis internus from the region mentioned above, and of the flexor tibialis externus, from the ilio-ischiadic ligament dorsal to the last mentioned.

These muscles have, for the most part, moved posteriorly or dorsally as expected. Pubo-ischio-tibialis, one of the most anterior members of this group, has been reduced, confined posteriorly to the ischium and, further, has moved dorsally to a position just below the acetabulum on the anterior edge of the ischium. In doing this it has not only entered between the two main heads of pubo-ischio-femoralis externus but, as its course shows, has broken in on to the ischium so as to separate the two heads of the adductor. One portion of flexor tibialis internus (1) is in its primitive position in the alligator; but in the Saurischia its origin is only about halfway down the posterior edge of the ischium. A second portion of flexor tibialis internus (2) has moved dorsally and gained an origin from the ilium.

Of the deeper set, the most anterior member, the pubo-tibialis, has disappeared entirely. The remaining members of the group are posterior and dorsal in position, flexor tibialis internus 3 having migrated up along the posterior margin of the ischium, part 4 having migrated up along the ilio-ischiadic ligament (in the Crocodilia at least; its existence in the Saurischia cannot, of course, be proved) and flexor tibialis externus having moved dorsally to the ilium.

The adductor musculature has also moved somewhat posteriorly and dorsally. It is divided into two portions, both arising from the ischium and not at all from the pubis. In the dinosaurs, the small size of the part of the ischium devoted to appendicular muscles has brought the adductors halfway from the original ventral line to the acetabulum. This is not true of the Crocodilia; but even here, by the division into two parts, both (especially the posterior) have pushed upwards on either side of pubo-ischio femoralis externus 3 so that they extend some distance dorsally along either edge of the ischium.

Pubo-ischio-femoralis externus, as has been mentioned above, cannot move dorsally. Its differentiation has consisted in a division into



two main portions, part 2 from the outer surface of the pubis, and part 3 from the outer surface of the ischium.

In addition, the Crocodilia possess an additional head (part 1) from the inner surface of the pubis, emerging (in contradistinction to pubo-ischio-femoralis internus) below, rather than above, the ambiens, and joining part 2, of which it is a derivative. This muscle is not found in other living reptiles; and it was apparently also absent in primitive forms. The region through which it passes from the internal to the external surface of the pubis is usually occupied by the insertion of the rectus in modern reptiles. In the Crocodilia, the rectus inserts mainly into the strong last abdominal rib and this leaves the edge of the pubis free for the passage of the muscle. Its existence depends then upon the presence of a strong abdominal rib paralleling the pubis. As far as I know, this condition is not found in the Saurischians. For example, a specimen of *Struthiomimus* in this museum has a well-preserved "abdominal basket," extending to the pelvis; but there is no noticeable strengthening posteriorly. In default of such evidence it seems probable that pubo-ischio-femoralis 1 of the Crocodilia was not present in the Saurischia.

As I have shown previously, the pubo-ischio-femoralis internus has retreated from the interior of the pubic region in the "Archosauria."

The ambiens remained in position near its primitive place of origin from the pubis near the acetabulum. The ischio-trochantericus also appears to have been unchanged. The coccygeo-femoral muscles appear to have been well developed. The "fourth trochanter" for the insertion of coccygeo-femoralis longus on to the femur is well marked. There is an excavation beneath the posterior end of the ilium for the origin of part of coccygeo-femoralis brevis.

In a number of cases areas of origin from the pubis and ischium are absolutely determinable in saurischian dinosaurs; and in every case they agree closely with the conditions found in the Crocodilia. The tendinous origin of flexor tibialis internus 3 is seen on almost every theropod pelvis; it was apparently a large muscle. That of flexor tibialis externus 1 is shown on several specimens. These two origins are also to be observed on a specimen of *Diplodocus* in this museum. In *Tyrannosaurus* an outward curving of the antero-ventral corner of the ischium is comparable to the region from which adductor 1 arises in the alligator. And in a mounted specimen of *Tyrannosaurus* the origin of pubo-ischio-tibialis may be seen. With these landmarks the areas of origin of pubo-ischio-femoralis externus 3 and adductor 2 may be determined with reasonable



accuracy. A tuberosity on the pubis (or pubis and ilium) is usually present and indicates the site of the ambiens.

In figures 4–8 a restoration of the pelvic musculature of *Tyrannosaurus* has been attempted. It is, of course, impossible to be sure of a number of points, such as the subdivisions of the ilio-tibialis or ambiens or the arrangement of the tendons at the knee. Where there has been doubt the crocodilian arrangement has been followed as being the most probable in

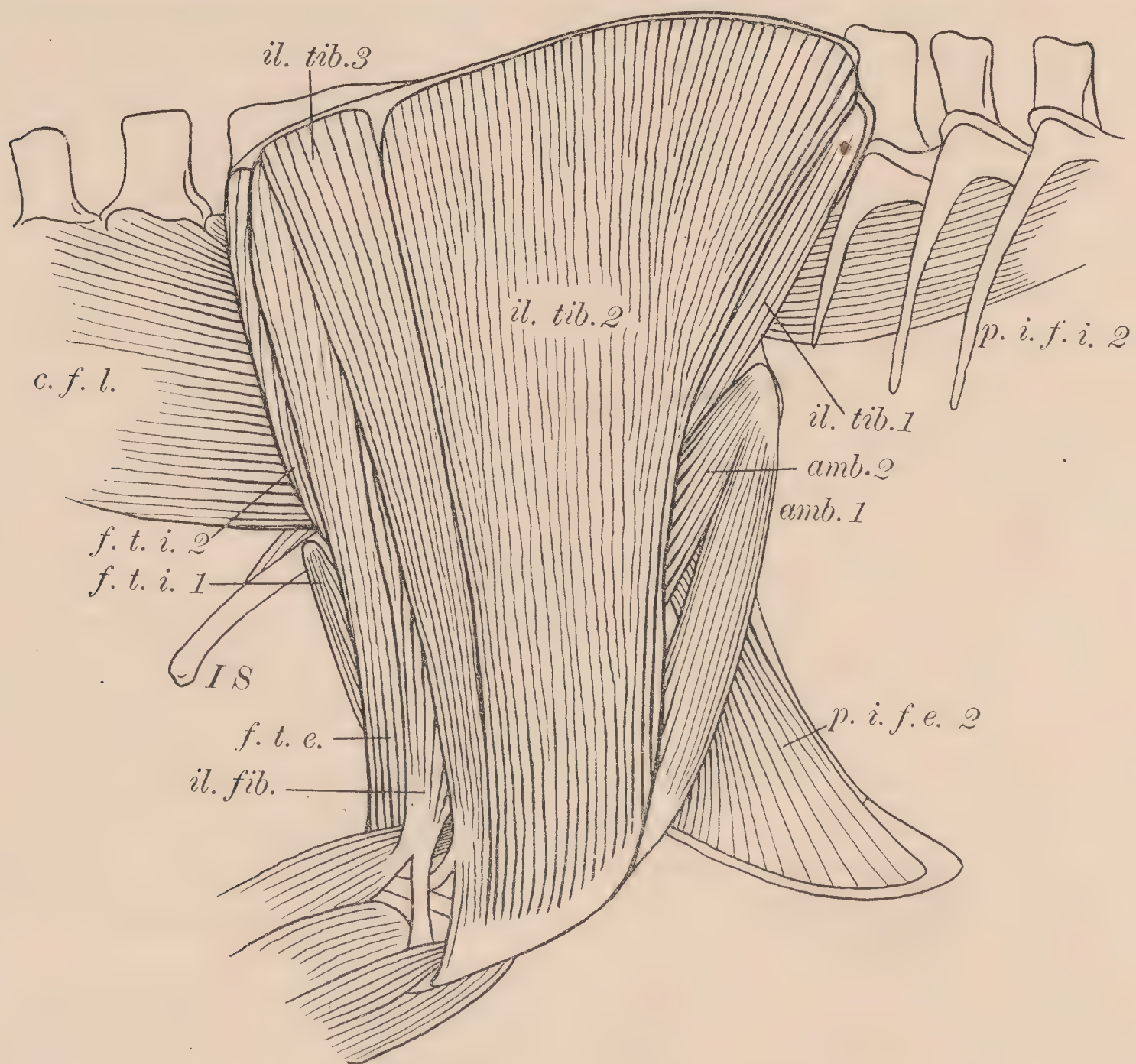


Fig. 4. Lateral view of pelvic region of *Tyrannosaurus* (right side) with the appendicular muscles restored. For abbreviations, see Fig. 2.

view of the close similarity in all known points. The muscles were restored in clay on a reduced model of the pelvic region. In the figures the axial musculature has been omitted to avoid too great a complexity. Its relations to the girdle are simple.

The dorsal musculature was primitively continuous, universally attaching itself to the inner surface of the ilium above the ribs and to the anterior (ilio-costalis) and posterior margins of this bone. This was true



of the sauropods and some theropods, as *Ornitholestes*. In *Tyrannosaurus* the two ilia are applied to the spines, separating caudal and trunk portions. Huge rugose surfaces on the posterior end of the ilium of *Brontosaurus* and *Tyrannosaurus* and surfaces on a line with these on the transverse processes of the caudal vertebræ indicate strong ligaments running longitudinally in this region and separating the dorsal tail

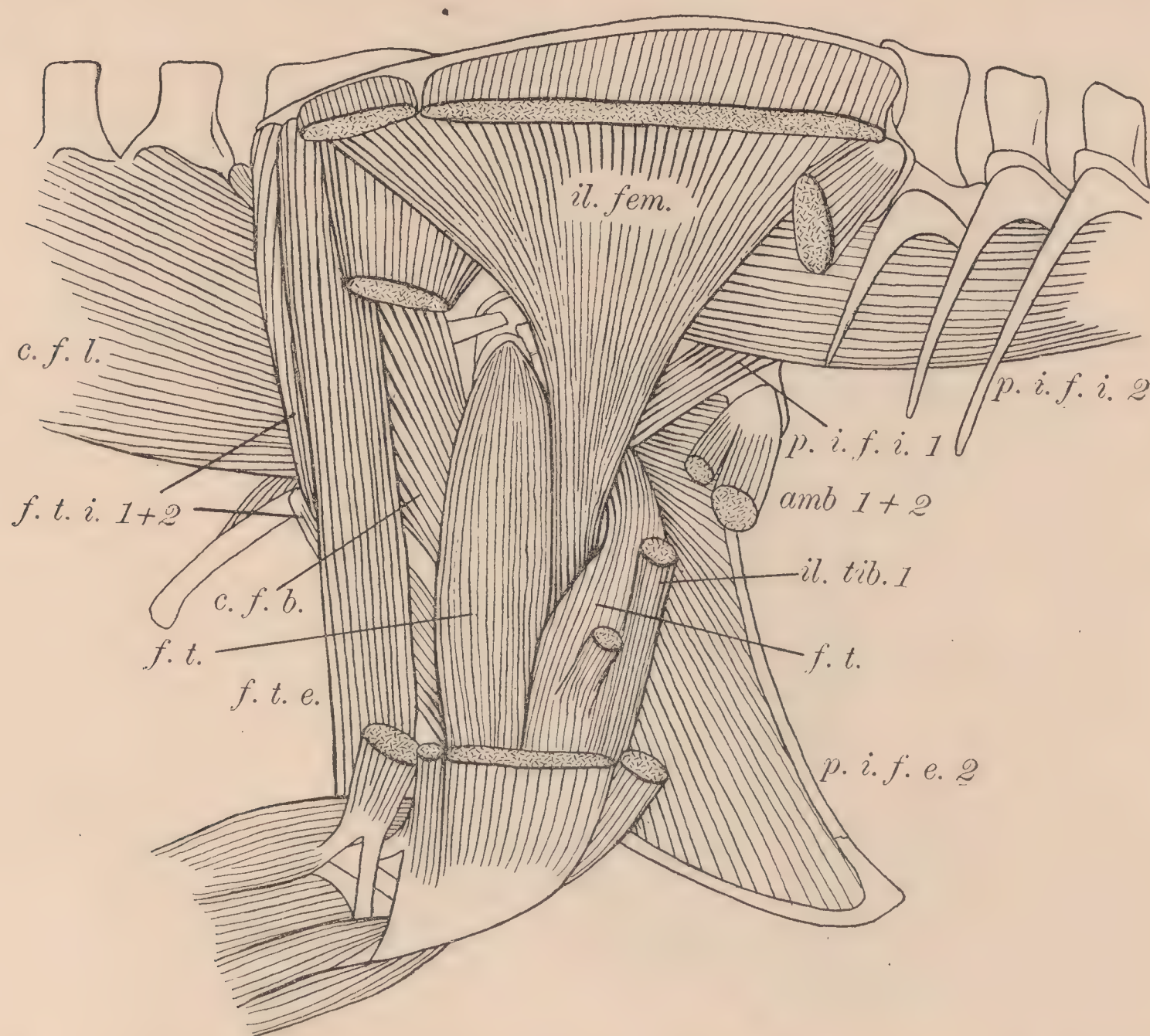


Fig. 5. Same as Fig. 4, but ilio-tibialis, ambiens and ilio-fibularis have been cut.

musculature (dorsalis caudæ) from the ventral (ilio-ischio-caudalis). The ilio-caudalis undoubtedly attached to the lower edge of this ligament and perhaps along its lower margin reached the ilium.

Antero-ventrally, the rectus attached to the extremity of the pubis, or rather its cartilaginous extension, and probably, as mentioned above, to the anterior edge of the body of the pubis. The obliquus externus probably attached tendinously in the neighborhood of the ambiens, as is usually the case in reptiles, and (through its connection with the rectus) to the pubis. Postero-ventrally, the ischio-caudalis arose from the distal portion of the ischium, as did undoubtedly part of the cloacal musculature.



A number of criticisms may be made of the restorations of the musculature of Triassic dinosaurs by Von Huene (1908); as I have mentioned most of these are due to our inadequate knowledge of the Crocodilia. On the ilium (p. 291) no origin is afforded for ilio-tibialis (except as we consider ilio-fibularis 1 as part of this muscle). Ilio-fibularis was probably farther posterior and ventral. Ilio-femoralis (externus) was prob-

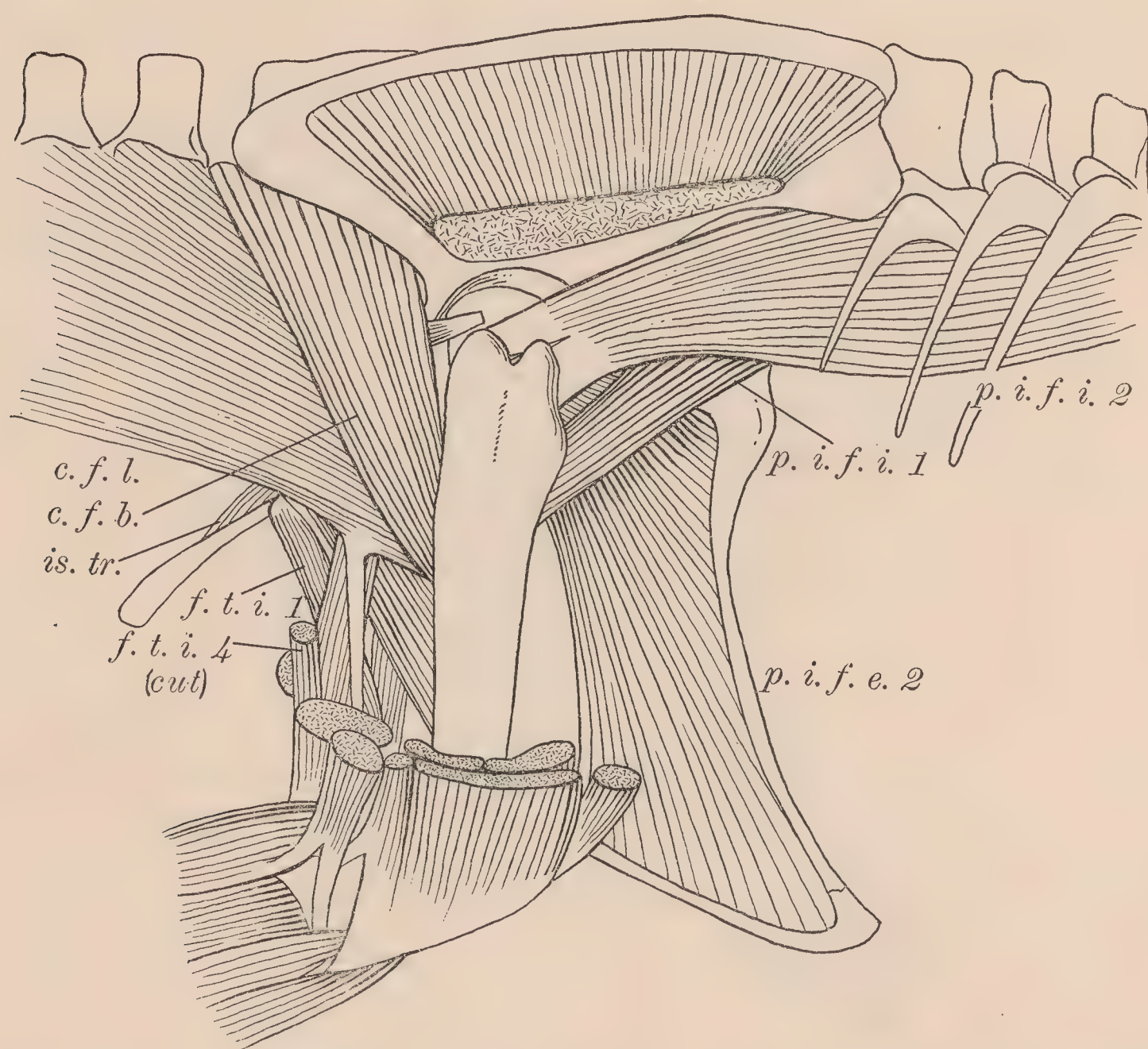


Fig. 6. Same as Fig. 5, with ilio-femoralis, flexor tibialis externus, flexor tibialis 2, and femoro-tibialis removed.

ably larger. On the pubis (p. 292) the "pubo-tibialis" insertion may have been either for part of ambiens or a tendon of the obliquus: there is no pubo-tibialis in the Crocodilia nor in birds. In regard to the ischium (p. 293) there is never, of course, any origin of the extensor ilio-tibialis from this bone. Pubo-ischio-femoralis externus (3) and ischio-femoralis (adductor 1) are correctly placed. Flexor tibialis internus 2 is incorrectly located, and locations for pubo-ischio-tibialis and flexor tibialis internus 1 and 3 of the writer are not indicated. Pubo-ischio-femoralis posterior, if equivalent to the writer's ischio-trochantericus,



should be on the upper internal instead of the ventral external portion of the bone. The ischio-caudalis should be restricted to the distal portion of the bone.

The femur (p. 295). The ilio-femoralis (externus), "quadratus lumborum," and pubo-ischio-femoralis posterior are shown attaching to the greater trochanter. The first is undoubtedly correct. "Quadratus

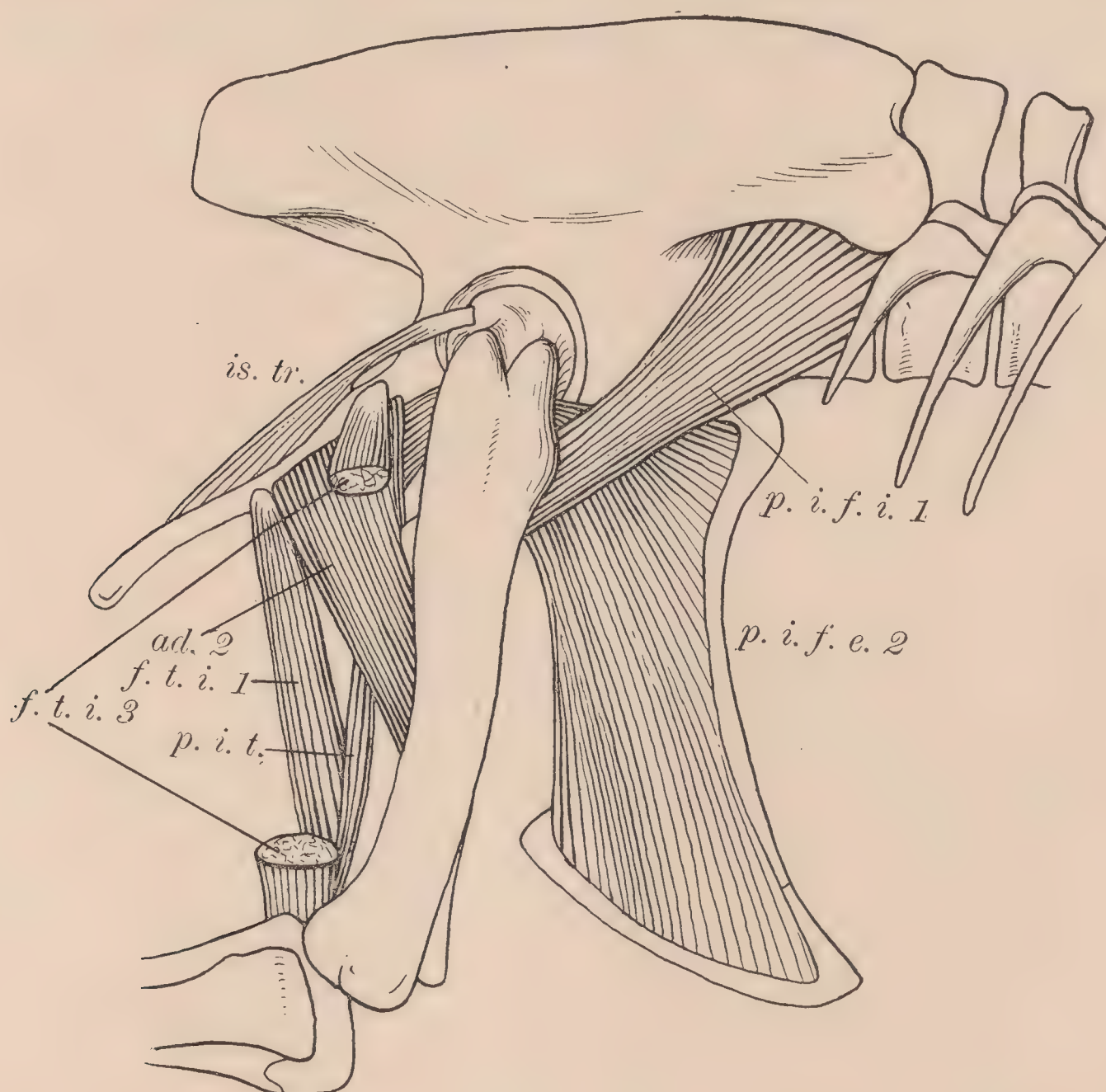


Fig. 7. Same as Fig. 6, with the coccygeo-femoralis, pubo-ischio-femoralis internus 2 and flexor tibialis internus 3 cut.

lumborum" (pubo-ischio-femoralis internus 2) runs beneath the ilio-femoralis in a direction opposite to that of the red arrow and probably inserted about, but not on, the trochanter. Caudo-ilio-femoralis (coccygeo-femoralis brevis) inserted more ventrally, about in the position of Von Huene's pubo-ischio-femoralis internus 3. The area occupied by femora-tibialis, to judge by either Crocodilia or birds, was much greater. I know of no part of pubo-ischio-femoralis internus likely to insert so far proximally as that shown in figure *b*. Of the muscles shown inserting on the fourth trochanter, probably only caudo-femoralis (coccygeo-



femoralis internus longus) should be placed there. The pubo-ischio-femoralis externus and that portion of pubo-ischio-femoralis which equals ischio-trochantericus inserted proximally to this trochanter. The adductors (ischio-femoralis and pubo-ischio-femoralis posterior in part) inserted about in the area marked "pubo-ischio-femoralis posterior zum Teil."

Most of the modifications of the tentative restoration of *Ornitholestes* by Gregory and Camp (1918), which might be suggested, are merely ones of nomenclature.

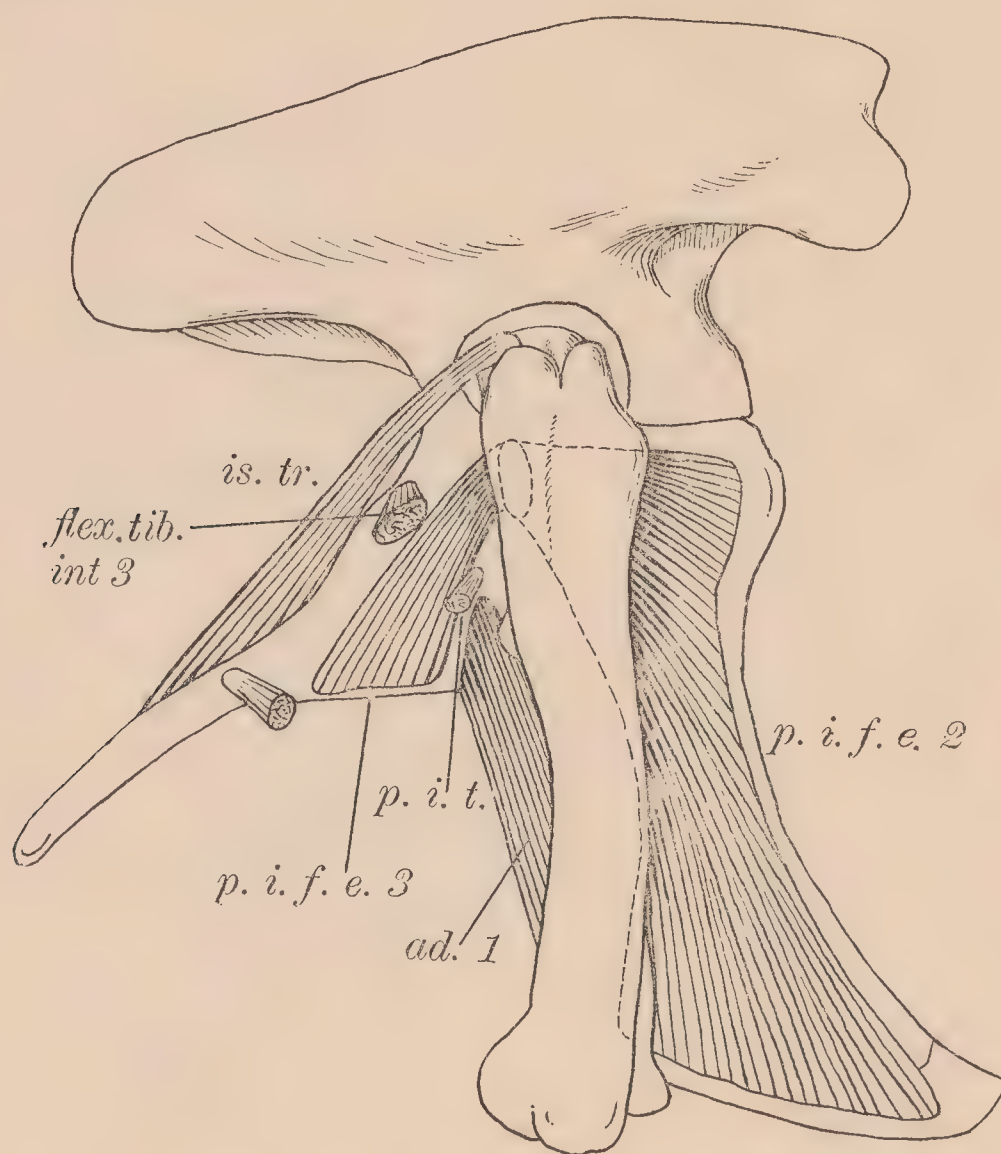


Fig. 8. Same as Fig. 7, from which adductor 2, the remaining flexors and pubo-ischio-femoralis internus 1 have been removed.

The question as to whether pubo-ischio-trochantericus internus (=pubo ischio-femoralis externus 1 of the Crocodilia) extended down the inner side of the pubis has been discussed above. "Adductor longus" = pubo-ischio-tibialis. The ridge below it was probably occupied by adductor 1. The space labeled ischio-femoralis was occupied by pubo-ischio-femoralis 3 and this probably extended anteriorly to include the excavation in the ischium, which is thus (as explained above) a close parallel to the "obturator fenestra." The posterior area marked pubo-ischio-femoralis externus is that for adductor femoris 2, except that the latter muscle probably did not extend so far distally. No area is marked



off for flexor tibialis internus 1. It seems probable that ilio-femoralis extended farther posteriorly.

Few criticisms may be made of the later restorations by Dr. Gregory shown in figure 1. Ilio-tibialis, ilio-femoralis, ilio-fibularis, flexor tibialis externus, caudi-ilio-femoralis (=coccygeo-femoralis brevis), "quadratus lumborum" (=pubo-ischio-femoralis internus), ambiens, the pubic head of pubo-ischio-femoralis externus, pubo-ischio-femoralis posterior (=ischio-trochantericus), and the iliac and one ischiadic head of flexor tibialis internus, I believe to be all correctly located. The question as to an internal pubic muscle has been mentioned previously. Adductor 2 probably occupied the proximal part of the area given the ischiadic head of pubo-ischio-femoralis externus. That muscle occupied most of the flat surface marked ischio-femoralis, the ischio-femoralis (adductor 1) lying slightly more anteriorly. Pubo-ischio-tibialis and flexor tibialis internus 1 are not located; the head of the latter muscle shown arising from beneath the posterior part of the ilium is probably incorrect.

#### SUMMARY

The evolution of the pelvis of saurischian dinosaurs is discussed. The marked change in the pubo-ischium is attributed to the changed position of the femur, which has resulted in a shifting of many muscles posteriorly and dorsally. The similarity of the saurischian musculature to that of the Crocodilia is pointed out. A restoration of the pelvic musculature of *Tyrannosaurus* is attempted.

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**Article XX.**—THE BRACHYURAN CRABS COLLECTED BY  
THE U. S. FISHERIES STEAMER 'ALBATROSS' IN 1911,  
CHIEFLY ON THE WEST COAST OF MEXICO<sup>1</sup>

BY MARY J. RATHBUN

PLATES XXVI TO XXXVI

The number of species in this list is 56, which by no means represents the existing fauna of the region. There are, however, a number of new and rare species which add value to the collection. A new species of *Sesarma* has already been described from Magdalena Bay, and the males of two unknown species of *Pinnotheres* are described below; these may later on be linked up with the females of the species, which are perhaps already described. The differences in shape and general appearance between males and females of this genus are usually too great for one to identify both sexes of a species unless they are found associated. A series of *Pilumnus* from Lower California enables the author to establish the presence of two closely allied species with continuous ranges which overlap at Magdalena Bay. The ranges of various species are extended, including those of *Lophopanopeus heathii*, *Panopeus bradleyi* and *Collodes tumidus*. Also noteworthy is the presence in the collection of a well-developed specimen of *Pliosoma parvifrons*, a species of rare occurrence.

A considerable collection of young stages, chiefly crab megalopa, was obtained. It is impossible to identify all of them with certainty, as our knowledge of the development of these creatures is still very limited. It has been thought best to publish drawings of the different forms, that future students who contrive to raise the young from the eggs may be able to classify them. The drawings of larvæ were made by Dr. Charles J. Fish, of the Bureau of Fisheries, who is making an intensive study of the plankton of the Woods Hole region. He has suggested the generic position of several of the Lower Californian larvæ which are akin to others on the Atlantic side.

**DROMIIDÆ**

***Dromidia larraburei* Rathbun**

*Dromidia sarraburei* (by error) RATHBUN, 1910, Proc. U. S. Nat. Mus., XXXVIII, October 20, p. 553, Pl. XLVIII, fig. 4.

<sup>1</sup>Scientific Results of the Expedition to the Gulf of California in charge of Dr. C. H. Townsend, by the U. S. Fisheries Steamship 'Albatross' in 1911; Commander G. H. Burrage, U. S. N., commanding. XIII. Published by permission of the U. S. Commissioner of Fisheries.



*Dromidia segnipes* WEYMOUTH, 1910, Leland Stanford Jr. Univ. Publ., Univ. Ser., No. 4, November 12, p. 15, Pl. I, figs. 1-2.

*Dromidia larraburei* SCHMITT, 1921, Univ. Calif. Publ. Zoöl., XXIII, p. 183, Pl. XXXIII, fig. 1.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 2 small ♀; one "had a large compound ascidian on its back."

Without locality label; 1 ♀, soft-shell.

See also list of larvæ.

### **Hypoconcha digueti** Bouvier

1898, Bull. Mus. Hist. Nat., Paris, IV, pp. 374 and 376.

San Estaban Island; 1 ♂ without chelipeds. Length of carapace 10.2 mm., width 10.6 mm.

The type female came from La Paz Bay.

### **CALAPPIDÆ**

#### **Cycloes bairdii** Stimpson

*Cyclois bairdii* STIMPSON, 1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 237 [109].

Cape San Lucas; March 23; 2 ♂ 1 ♀.

### **PORTUNIDÆ**

#### **Portunus (Portunus) xantusii** (Stimpson)

*Achelous xantusii* STIMPSON, 1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 222 [94].

Point San Bartholome; 2 juv. Also with boat dredge; March 13; 3 ♂ 5 ♀.

Santa Maria Bay; boat dredge; March 18; 100 juv.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 1 ♂ 1 ♀.

Cape San Lucas; March 23; 6 ♂ 8 ♀ (2 ovigerous).

Pichilique Bay: By electric light; March 27; 6 ♂ 1 ♀ 16 juv. April 18; 6 ♂ 1 ovigerous ♀. By electric light; 1 juv.

San Josef Island; March 31; 1 ♂ 1 ♀.

Agua Verde Bay; April 1; 1 juv.

Without locality label; 59 juv.

#### **Arenæus mexicanus** (Gerstæcker)

*Euctenota mexicana* GERSTÆCKER, 1856, Arch. f. Naturg., XXII, pt. 1, p. 131, Pl. v, figs. 3 and 4.

Ballenas Bay; March 16; 1 ♂ 1 ♀.



**Callinectes arcuatus** Ordway

1863, Boston Journ. Nat. Hist., VII, p. 578.

San Jose del Cabo; March 26; 2 ♂ 2 ♀ (1 immature, 1 soft-shell).

**Callinectes bellicosus** (Stimpson)

*Lupa bellicosa* STIMPSON, 1859, Ann. Lyc. Nat. Hist. N. Y., VII, p. 57 [11].

Point San Bartholome: With boat dredge; March 13; 3 ♂ 2 ♀.  
March 14; 1 ♂. In seine; 4 juv.

Abreojos Point; March 16; 2 ♀.

Ballenas Bay; March 16; 2 ♂ juv., 1 ♀ juv.

S. end of Magdalena Bay; March 20; 10 ♂ 2 ♀.

Pichilique Bay: By electric light; March 27; 6 juv. March 29;  
1 ♂ juv.

Agua Verde Bay; April 2; 2 immature ♀.

Mulege, at mouth of river; in 100-foot seine; April 4; 1 ♂.

Ricason Island, Concepcion Bay; April 7; 8 ♂ 2 ♀.

**Cronius ruber** (Lamarck)

*Portunus ruber* LAMARCK, 1818, 'Hist. Nat. Anim. sans Vert.,' V, p. 260.

*Amphitrite edwardsii* LOCKINGTON, 1877, Proc. Calif. Acad. Sci., VII, 1876, p. 43 [3].

Point San Bartholome; in seine; March 14; 2 ♂ 2 ♀.

**ATELECYCLIDÆ****Pliosoma parvifrons** Stimpson

Plate XXVI

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 228 [100], Pl. III, fig. 6.

Cape San Lucas; March 23; 1 ♂. Carapace 20 mm. long, 18.8 mm. wide.

The specimen is larger than those collected by Xantus and is better developed. The spines are reduced in size, the gastric, hepatic and two inner branchial prominences being scarcely more than tubercles. The first ambulatory leg is nearly twice as long as the carapace; the cheliped is stronger than the legs and one and two-thirds times as long as the carapace; surface finely granulate except on distal half of fingers; merus subcylindrical, carpus subspherical; propodus a little compressed, increasing in width gradually and regularly almost to the fingers where the lower margin bows outward, giving the fixed finger a sinuous edge and making a considerable gape between the proximal halves of the fingers, into which a very low, broad tooth projects from the dactylus; meeting edges crenulate.



**CANCRIDÆ****Cancer jordani** Rathbun

1900, Amer. Nat., XXXIV, p. 133.

Middle of east side of Cerros Island; March 12; 1 ♀.

**Cancer amphicetus** Rathbun

1898, Proc. U. S. Nat. Mus., XXI, p. 582.

Middle of east side of Cerros Island; March 12; 1 juv.

Santa Maria Bay; with boat dredge; March 18; 2 juv.

**XANTHIDÆ****Leptodius occidentalis** (Stimpson)

*Chlorodius occidentalis* STIMPSON, 1871, Ann. Lyc. Nat. Hist. N. Y., X, p. 108.

Pichilique Bay; March 27; 5 ♂ 3 ♀.

Agua Verde Bay; April 1; 3 ♂.

**Xanthodius hebes** Stimpson

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 208 [80].

Pichilique Bay; March 27 and 29; 16 ♂ 17 ♀.

Agua Verde Bay; April 1; 2 ♂ 8 ♀ (1 ovigerous).

San Francisquito Bay; April 9; 1 ♀.

**Cycloxanthops novemdentatus** (Lockington)

*Xanthodes? novem-dentatus* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876, p. 32.

Point San Bartholome; in seine; 1 ♀.

**Glyptoxanthus labyrinthicus** (Stimpson)

*Actæa labyrinthica* STIMPSON, 1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 204.

San Francisquito Bay; beach; April 9; 1 ♂.

**Panopeus bradleyi** Smith

1869, Proc. Boston Soc. Nat. Hist., XII, p. 281.

Santa Maria Bay; with boat dredge; March 18; 1 ♀.

Head of Concepcion Bay; April 6; 1 ♂.

**Eurypanopeus planissimus** (Stimpson)

*Xantho planissima* STIMPSON, 1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 205.

Agua Verde Bay; April 1; 1 ♂.

San Francisquito Bay; beach; April 9; 4 ♂.



***Micropanope nitida* Rathbun**

1898, Proc. U. S. Nat. Mus., XXI, p. 587, Pl. XLII, fig. 9.

Agua Verde Bay; April 1; 1 ♂ 3 ♀.

Locality not given; 23 ♂ 16 ♀ 1 juv.

***Lophopanopeus heathii* Rathbun**

1900, Amer. Nat., XXXIV, p. 137.

Middle of east side of Cerros Island; March 12; 1 ♂ and carapace.

***Pilumnus spinohirsutus* (Lockington)**

Plate XXVII

*Acanthus spino-hirsutus* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876 pp. 33 and 102.

*Pilumnus spino-hirsutus* STREETS AND KINGSLEY, 1877, Bull. Essex Inst., IX, p. 107.

*Pilumnus spinohirsutus* RATHBUN, 1904, 'Harriman Alaska Exped.,' X, p. 185 (part), not Pl. VII, fig. 2; 1910, Proc. U. S. Nat. Mus., XXXVIII, p. 585 (part).

Point Abrejos; March 6; 1 ♂.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 1 ♂ 1 ♀ 2 juv.

Occurs in southern California and on the west coast of Lower California as far south as Magdalena Bay.

From Magdalena Bay southward as far as Manzanillo, including the Gulf of California, *P. spinohirsutus* is replaced by a form which I formerly regarded as a variation, but a considerable series of both sorts from many localities shows consistent differences.

Lockington's types are not extant. His description would apply to either species, according to the reader's interpretation of this sentence: ". . . four larger spines on antero-lateral margin of carapax, besides those on upper margin of orbit." Did he include the spine at the outer angle of the orbit with the antero-lateral spines or with the upper orbital spines? We can judge only by the locality of his specimens, San Diego, which is included in the range of the northern species, and from which the National Museum possesses two specimens belonging to that species. In it, there are four antero-lateral spines beside the outer orbital spine; the latter therefore was classed by Lockington with "those on upper margin of orbit."

The species have much in common. In both, the dorsal surface of carapace and appendages is covered with long hairs, except the hinder part of the carapace, while the carapace and ambulatory legs have a short



coat of pubescence. The carapace is very convex antero-posteriorly, slightly convex from side to side. The antero-lateral margins are armed with long spines, the orbit and the front with shorter spines. Chelipeds spinous above and also on the outer surface of the palms except on the lower portion of the larger palm. On the legs, the upper surface of the carpus-propodus and the distal extremity of the merus are spined.

The differences are as follows:

*P. spinohirsutus*

Antero-lateral spines 5; the first or orbital spine is a little shorter than the others and the space between first and second is less than the other spaces, the bases of those spines often contiguous, so that they appear like one deeply bifid spine.

No subhepatic spine, although there may be some small spinules.

Frontal spines short.

In male usually half of outer surface of larger hand is smooth and naked, the smooth area separated obliquely from the rough area by a line running from the lower proximal corner to the distal end opposite the middle of base of dactylus. In female the smooth space is similar to, but smaller than, that of the male.

Carapace wider, width (exclusive of spines) more than  $1\frac{1}{3}$  times length.

*P. townsendi*

Antero-lateral spines 4, equally separated.

A slender, well-marked, subhepatic spine, below the interval between first and second lateral spines.

Frontal spines longer.

In both sexes less than half of outer surface of larger hand is smooth. A continuous line of short, conical spines runs lengthwise in line with the base of cutting edge of propodal finger.

Carapace narrower, width (exclusive of spines)  $1\frac{1}{3}$ , or less than  $1\frac{1}{3}$ , times length.

*P. spinohirsutus* runs larger than the next species, measuring 23.4 mm. (Cat. No. 32964, U. S. N. M.) in total length of carapace as contrasted with 14.2 in *townsendi* (type).

*P. spinohirsutus* shows a tendency to produce a posterior branch on the third lateral spines.

***Pilumnus townsendi*,<sup>1</sup> new species**

Plate XXVIII

*Pilumnus spinohirsutus* RATHBUN, not Lockington, 1904, 'Harriman Alaska Exped.,' X, p. 185 (part), Pl. VII, fig. 2; 1910, Proc. U. S. Nat. Mus., XXXVIII, p. 585 (part).

<sup>1</sup>For Dr. Charles H. Townsend, in charge of the 1911 expedition.



TYPE-LOCALITY.—Off Adair Bay, Gulf of California, Mexico; 17 fathoms; station 3026, 'Albatross'; 2 females (1 is holotype).

TYPE.—Cat. No. 17413, U. S. N. M.

MEASUREMENTS.—Female holotype, length of carapace on median line 13.8, length including spines 14.2, width excluding spines 18.3, including spines 21.4 mm.

SPECIMENS COLLECTED BY THE 1911 EXPEDITION.—

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 1 ♂ 1 ♀.

Head of Concepcion Bay; April 6; 1 ♂ 3 juv.

A lot containing 1 ♀, 3 juv., is labeled "Station 5695," obviously incorrect, as the depth at that station is 534 fathoms.

RANGE.—Magdalena Bay to Manzanillo, via Gulf of California, to a depth of 22 fathoms.

For description of this species and its relations, see under *Pilumnus spinohirsutus*, above.

#### ***Pilumnus gonzalensis* Rathbun**

1893, Proc. U. S. Nat. Mus., XVI, p. 240.

San Francisquito Bay; April 9; 2 ♀.

#### ***Eurytium affine* (Streets and Kingsley)**

*Panopeus affinis* STREETS AND KINGSLEY, 1877, Bull. Essex. Inst., IX, p. 106.

Pichilique Bay; March 27; 3 ♂ 1 ♀.

#### ***Eriphia squamata* Stimpson**

1859, Ann. Lyc. Nat. Hist. N. Y., VII, p. 56 [10].

Agua Verde Bay; April 1; 1 ♂ 1 ♀.

Pichilique Bay; March 27; 5 ♂ 8 ♀ (3 ovigerous).

Mazatlan; 1 propodus of right cheliped.

#### **PINNOTHERIDÆ**

##### ***Pinnotheres jamesi*,<sup>1</sup> new species**

Plate XXIX, Text Figures 1 and 2

TYPE-LOCALITY.—Pichilique Bay, Lower California; by electric light; 1 male.

TYPE.—Cat. No. 57005, U. S. N. M.

MEASUREMENTS.—Length of carapace of type male 3.7 mm., width the same.

DIAGNOSIS OF MALE.—Carapace hard, nearly circular, bordered with hair around lateral angles. Last leg very much smaller than the others. Male abdomen extremely long and narrow.

DESCRIPTION OF MALE.—Carapace subcircular, inclining toward the hexagonal, broadest at the middle of its length; evenly convex in all directions; surface smooth and shining except for a narrow border of pubescence, 1.4 mm. long, embracing the

<sup>1</sup>For Mr. Arthur Curtiss James, a patron of the expedition.



widest part of the carapace. Posterior margin 2.3 mm. long, slightly curved; posterolateral margin thickened over the last pair of legs. Front 1.2 mm. wide, nearly truncate; extremities curved; middle part bent under and ending in a point.

Chelipeds shorter than first leg and very little stouter. Margins of chelipeds and legs hairy. Palm increasing in width distally; fingers with a small tooth near base of inner edges, tips curved toward each other. The legs are similar in form, their relative lengths represented by 2.3.1.4, the second longest, fourth very much shorter than the others, its merus not reaching the middle of the merus of the third leg; in all, the margins of the merus are subparallel, the upper margin of the propodus is slightly arched, the dactylus is strongly curved, gradually tapering, but with a very slender tip; the carpus-propodus of the second and third legs has a fringe of long hairs on the posterior surface which proceed from near the upper margin.

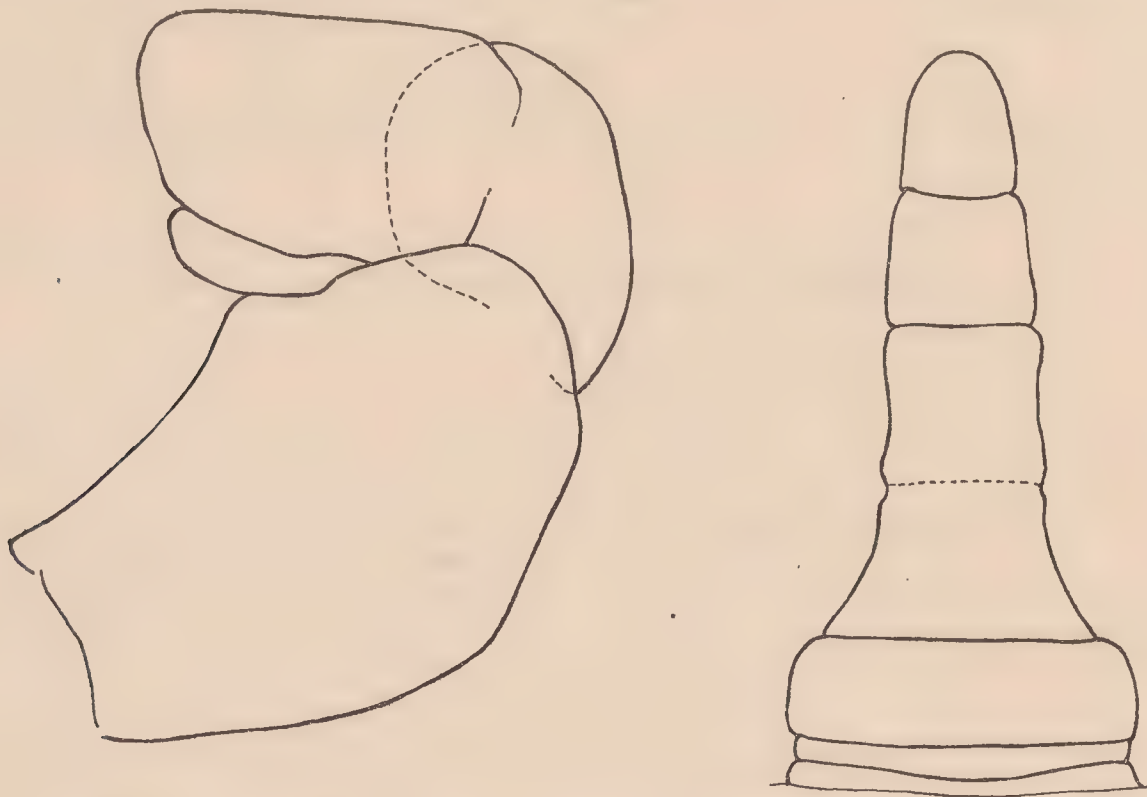


Fig. 1. *Pinnotheres jamesi*, left outer maxilliped of ♂ holotype,  $\times 77.5$ .

Fig. 2. *Pinnotheres jamesi*, abdomen of ♂ holotype,  $\times 18$ .

The abdomen is very narrow and long, reaching to the buccal cavity; the first two segments are linear, the third occupies little more than half the width of the sternum, its ends rounded; fourth and fifth segments fused, the line of union partially visible; the fourth tapers a little, the fifth is nearly square; the sixth is a little shorter than the fifth and narrows slightly to the seventh, which is suboblong with rounded tip.

This species belongs to the same group as *P. concharum*<sup>1</sup>; it differs from male *concharum* in its rounder carapace with pubescence along the lateral angles instead of around the anterior half of the carapace, in the broader front, the more convex posterior margin, the shorter and broader legs, especially noticeable in the propodus, the longer and differently shaped abdomen. The outer maxilliped is akin to that of *P. reticulatus*,<sup>2</sup> from the Gulf of California, which is known only from the female and has no other obvious relation to *P. jamesi*.

<sup>1</sup>Rathbun, 1918, Bull. U. S. Nat. Mus., No. 97, p. 86, Pl. xx, figs. 3-6, text-fig. 42.

<sup>2</sup>*Op. cit.*, p. 93, Pl. xxi, figs. 1 and 2.



***Pinnotheres pichilinquai*, new species**

Plate XXX; Text Figures 3 to 5

TYPE-LOCALITY.—Pichilinqué Bay, Lower California; by electric light; March 27; 4 males.

TYPE.—Cat. No. 57004, U. S. N. M.

MEASUREMENTS.—Length of carapace of type male 4.4 mm., width 4.3 mm.

DIAGNOSIS OF MALE.—Pubescent. Carapace deeply sculptured. Chelipeds very heavy. Legs subequal.

DESCRIPTION OF MALE.—Carapace subhexagonal, the postero-lateral regions deeply hollowed, the posterior ambulatory leg fitting into the hollow; surface covered with a dense soft pubescence which forms a smooth, as opposed to a ragged, surface, but does not conceal the inequalities of the shell. Cardiac region surrounded by a deep groove except posteriorly; branchial and gastric regions grooved in such a

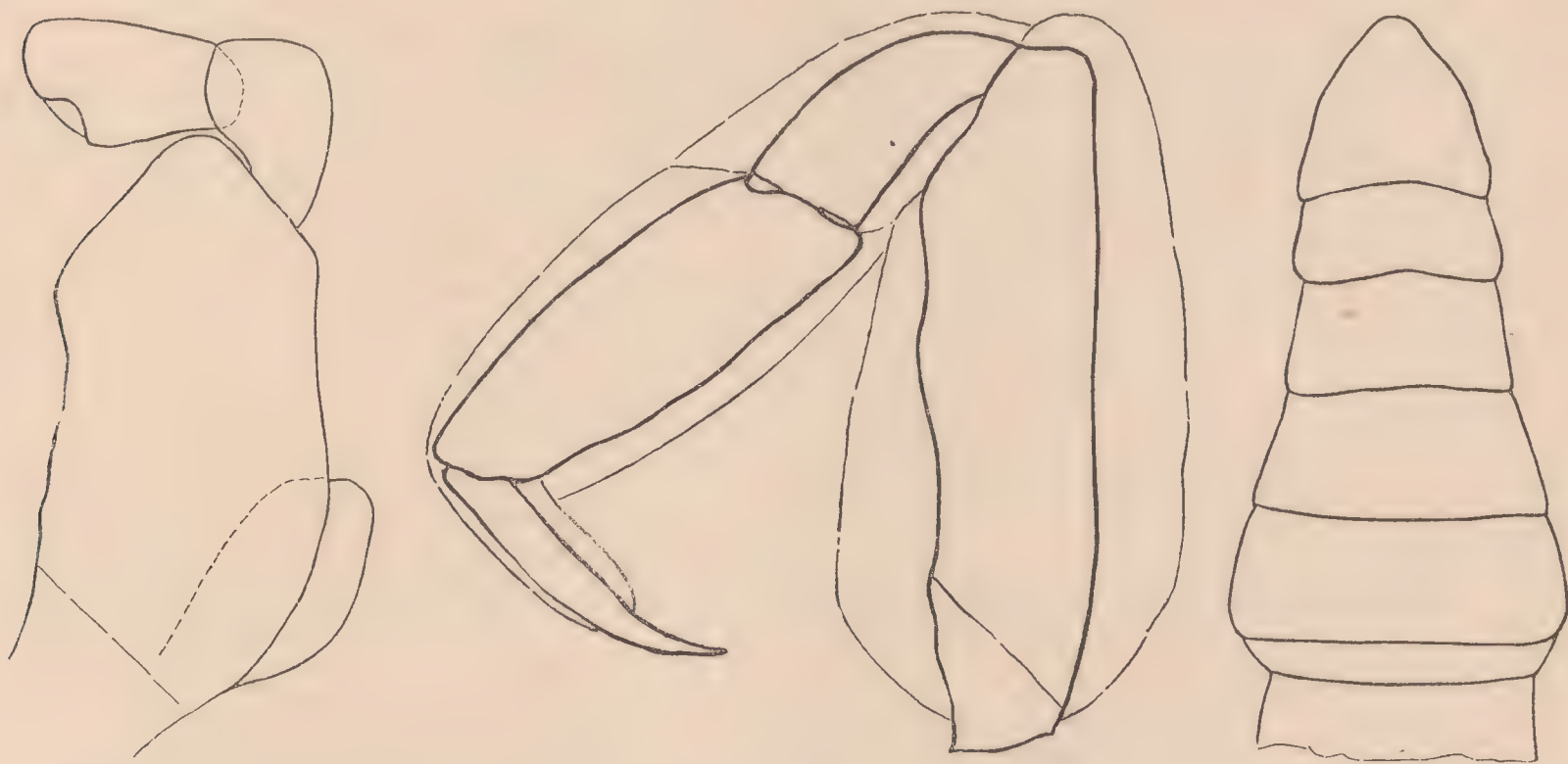


Fig. 3. *Pinnotheres pichilinquai*, left outer maxilliped of ♂ paratype,  $\times 33\frac{1}{3}$ .

Fig. 4. *Pinnotheres pichilinquai*, right first ambulatory leg of ♂ paratype,  $\times 27$ . The outer line marks the extent of the fringe of hair.

Fig. 5. *Pinnotheres pichilinquai*, abdomen of ♂ paratype,  $\times 27$ .

way as to form a regular pattern; hepatic region depressed. Front viewed from above, advanced, broadly subtriangular, edge arcuate; viewed from before, the front is deflexed and pointed. Orbits round, eyestalks stout, corneæ smaller but of good size and black. Antennules when folded bulging; antennæ as long as one-half width of front.

Chelipeds pubescent like the carapace and with a dense short fringe on the inner border; they are stout; carpus somewhat nodose, chela thick and high; palm with upper surface concave, outer surface with two longitudinal grooves; lower margin of propodus convex from one end to the other; fingers heavy, meeting when closed, tips slender and crossing; a small tooth near base of each finger.

Ambulatory legs similar, diminishing slightly from first to fourth pair; carpus-propodus broader than merus, and having a fringe of long hairs attached on the posterior surface just below the upper margin, the hairs lying against the surface; dactyli slender, long, curved.



COLOR.—The preserved specimens show a great deal of dark color on the carapace; in the type-specimen the front is light with a narrow, dark, median line, the extreme rear is light, the remainder is dark shading to nearly black; chelipeds and legs mostly light.

This is the Pacific counterpart of *P. shoemakeri*<sup>1</sup> which inhabits the Gulf of Mexico and the West Indies. The Atlantic species has a longer carapace with smaller areoles and wider furrows; the fingers are narrower and the legs much slenderer.

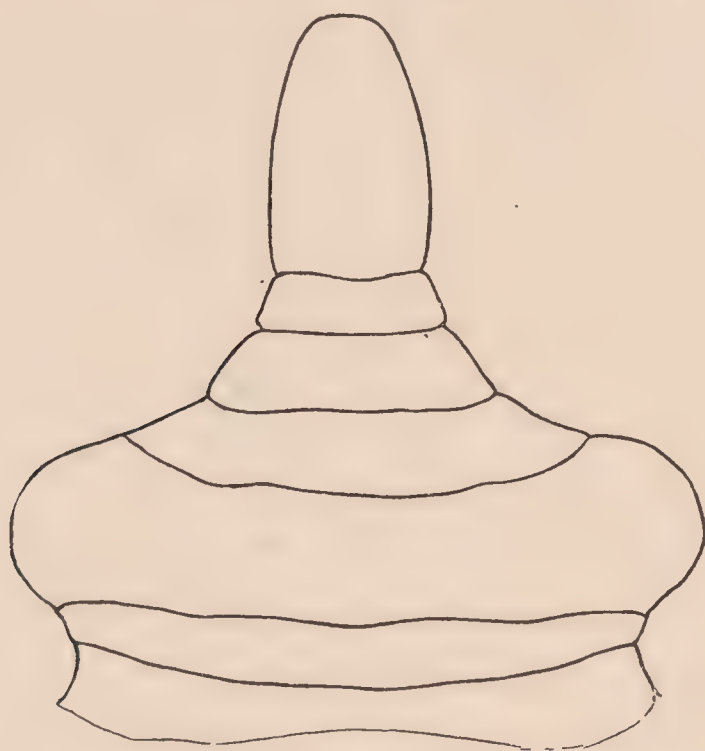


Fig. 6. *Parapinnixa nitida*, Pichilique Bay, abdomen of ♂, × 27.

***Parapinnixa nitida* (Lockington)**

Text Figure 6

*Pinnixa* (?) *nitida* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876, p. 155 [11], part (type-locality, Angeles Bay).

*Parapinnixa nitida* RATHBUN, 1918, Bull. U. S. Nat. Mus., No. 96, p. 107, text-fig. 58, and synonymy.

Pichilique Bay; by electric light; 1 ♂.

Carapace 2.6 mm. long, 5.6 mm. wide. The male is similar in shape to the female which is known to us only through Holmes's figure, the type specimen itself being no longer extant. Just behind the front there is a transverse furrow which laterally curves forward until it meets the upper margin of the orbit. The carpus and propodus, taken together, are more nearly of a size in the first three ambulatory legs than is represented in Holmes's figure where the second and third legs were narrowed by perspective.

<sup>1</sup>Rathbun, 1918, Bull. U. S. Nat. Mus., No. 97, p. 95, Pl. xxii, figs. 1-4, text-fig. 48.



**Dissodactylus nitidus** Smith

1870, Trans. Connecticut Acad. Arts and Sci., II, p. 173.

Santa Maria Bay; from boat dredge; March 18; 6 ♂ 2 ♀.

**GRAPSIDÆ****Grapsus grapsus** (Linnæus)

*Cancer grapsus* LINNÆUS, 1758, 'Sys. Nat.,' 10 Ed., I, p. 630.

South end of Cerros Island; March 10; 1 ♂.

Santa Maria Bay; March 18; 2 ♂.

San Estaban Island; April 13; 1 ♂.

Label illegible; 1 ♂.

**Geograpsus lividus** (Milne Edwards)

*Grapsus lividus* MILNE EDWARDS, 1837, 'Hist. Nat. Crust.,' II, 1837, p. 85.

Pichilique Bay; March 27; 2 ♀ (1 ovigerous).

**Pachygrapsus crassipes** Randall

1840, Journ. Acad. Nat. Sci. Philadelphia, VIII, 1839, p. 127.

Guadalupe Island; March 2; 1 ♂ 1 ♀.

E. San Benito Island; March 9; 1 ♂ 2 ♀ (1 ovigerous).

W. San Benito Island; March 9; 4 ♂ 2 ♀.

S. end of Cerros Island; March 10; 6 ♂ 8 ♀.

Santa Maria Bay; March 15; 1 ♂.

Point Abreojos; March 16; 1 ♂ 3 ♀ (1 soft-shell).

Margarita Island; March 19; 3 ♀.

Tiburon Island; April 12; 1 ♀.

**Pachygrapsus transversus** (Gibbes)

*Grapsus transversus* GIBBES, 1850, Proc. Amer. Assoc. Adv. Sci., III, p. 181.

Pichilique Bay; March 27; 1 ovigerous ♀.

Agua Verde Bay; April 1; 2 ♂ 1 ovigerous ♀.

**Goetice americanus**, new species<sup>1</sup>

Plate XXXI; Text Figure 7

*Hemigrapsus oregonensis* RATHBUN, Bull. U. S. Nat. Mus., No. 97, p. 270 (part).

TYPE-LOCALITY.—San Luis Gonzales Bay, Lower California (gulf side), Mexico; March 27, 1889; 'Albatross'; 70 males; 41 females (27 ovigerous). One male is holotype. A set of paratypes has been placed in the American Museum.

TYPE.—Cat. No. 17452, U. S. N. M.

<sup>1</sup>Not represented in the 1911 collection. Published here by permission of the Smithsonian Institution.



MEASUREMENTS.—Male holotype, length of carapace 14, greatest width 15.8, width between outer orbital angles 14.4 mm.

DESCRIPTION.—Dorsal aspect very much as in *Hemigrapsus oregonensis*. In specimens of equal carapace length, the width is a little less, both at the widest part and at the orbital angles, than it is in *oregonensis*, the posterior of the lateral teeth is smaller, the granulated ridge setting off the steep postero-lateral region is fainter, the blunt ridge just above and parallel to the margin of the front is more extensive, punctate and smoother than in *oregonensis*.

The most noticeable difference in the species is in the outer maxillipeds; the ischium is distinctly smaller than the merus and diminishes in width from the distal to the proximal end, its distal margin is concave forward except for a smooth arcuate lobe at the inner end which is strongly produced forward and partially overlaps the merus; merus elongate; palpus strongly developed, reaching, when it is folded in place, quite to the ischium.



Fig. 7. *Goetice americanus*, left outer maxilliped of ♂ paratype (Cat. No. 17452, U. S. N. M.),  $\times 8$ .

The chelipeds in the well-developed male are very heavy and equal; palms high height greater than length measured from articulation with carpus to sinus between fingers; anterior margin of palm very oblique; tip of immovable finger curved upward, wider than tip of dactylus; dactylus slender, a large lobe near its base, the distal half of which has a crenulated edge, continued also along the edge of the dactyl as far as the tip; a large brush of coarse hair occupies the greater part of the inner surface of the palm.

Ambulatory legs of moderate size and bordered with long, soft hair.

Abdomen of male narrow, the sides converging little from the third to the middle of the sixth segment.

VARIATION.—There is considerable variation in individuals from the same locality. Large specimens have not always as well developed chelipeds as smaller specimens. The two chelipeds may be unlike, one with a tooth on the dactyl, the other without a tooth, and with meeting fingers, similar to those of females and young. Most of the specimens of the type lot including all the females are devoid of hair on the legs; in a lot from Guaymas, there is a greater proportion of hairy individuals, including some females.



RANGE.—From San Bartolome Bay, on the west coast of Lower California to the Gulf of California where it has been found at Guaymas, Puerto Refugio on Angel Island, and at San Luis Gonzales Bay. It was not taken by the 1911 expedition of the 'Albatross.'

*Hemigrapsus oregonensis*, with which this species was formerly confounded, does not occur in Mexico farther south than Todos Santos Bay on the west coast of Lower California just below the United States line (not Todos Santos near the tip of the peninsula).

The genus *Goetice*,<sup>1</sup> distinguished by the form of the outer maxillipeds, has not before been noted in America. Its type species, *G. depressus* (de Haan),<sup>2</sup> is a common shore crab in Japan; it differs from the American species in its carapace narrowed behind instead of squarish and the articulation of merus and ischium of endognath of outer maxillipeds more oblique. Male abdomen and chelipeds similar, except that the inner surface of the palm is bare in *depressus*.

***Sesarma (holometopus) magdalenense* Rathbun**

Plate XXXII

1918, Bull. U. S. Nat. Mus., No. 97, p. 305, Pl. LXXXVI.

TYPE-LOCALITY.—Mangrove Island, Magdalena Bay, Lower California; March 20, 1911; 'Albatross'; 8 ♂ 8 ♀ (1 ♂ is type).

TYPE.—Cat. No. 45793, U. S. N. M.

MEASUREMENTS.—Type male, length of carapace 11.6 mm., width between the outer angles of the orbits 14.2 mm., width at postero-lateral angles 13.1 mm.

Carapace distinctly broader than long, broadest at the outer angles of the orbit, diminishing posteriorly, a very shallow sinus in the lateral margins behind the antero-lateral angles. Surface for the most part smooth and shining, depressions moderately deep; pits of two sorts, a few large scattered ones visible to the naked eye, and numerous small ones, which become crowded on the anterior branchial region. On the anterior and antero-lateral regions, there are a few scale-like granules. Antero-lateral angle a well-marked tooth.

Front about three-fifths as wide as carapace, surface nearly vertical, with the lower edge advanced; front widening below, lower margin arcuate, outer corners rounded; surface uneven, wrinkled and unevenly granulate with fine, depressed granules; superior frontal lobes nearly smooth and feebly separated, the middle pair the wider.

Chelipeds of male massive; merus and carpus covered on the outer surface with short granulated rugæ; chelæ high, swollen; immovable finger short, high, horizontal; dactylus strongly arched. Palm with lower margin very arcuate, its upper surface with several longitudinal, broken lines of fine granules, its outer surface, as well as the upper surface of the proximal half of the dactylus, covered with fine scabrous granules; fingers punctate, gaping; basal half of prehensile edge of the

<sup>1</sup>Gistel, 'Natur. Thierreichs,' 1848, p. x.

<sup>2</sup>*Grapsus (Platynotus) depressus* de Haan, 'Fauna Japon., Crust.,' 1835, p. 63, Pl. VIII, fig. 2, Pl. D (mouth-parts, *Platynotus*).



dactylus cut out in a deep sinus, into which projects a crenulated tooth of the immovable finger; both fingers irregularly dentate.

The chelipeds of the female have both fingers horizontal and longer than the immovable finger of the male; they do not gape, and the teeth fit rather closely together. In the young male the chelæ are intermediate in form between those of the adult male and of the female, and the gape is lacking.

Ambulatory legs with merus-joints rather short, (in the fourth pair  $2\frac{1}{4}$  times as wide as long), widening distally, and crossed by fine short rugæ; dactyli slender, longer than their respective propodi measured on the outer or anterior margin.

Abdomen of male broadly triangular; terminal segment as broad as long. Appendages of first segment rather slender, tips oblique.

COLOR.—Specimens preserved in alcohol have a greenish-blue carapace mottled with purple; upper, proximal half of chelæ reddish-brown; upper surface of legs covered with a pattern of fine dots of dark purple on a light ground.

This species is unlike other American *Sesarmæ* in its faintly marked frontal lobes, which give it much the appearance of a *Metasesarma*, e.g., *M. rousseauxi* Milne Edwards<sup>1</sup> and *M. aubryi* (A. Milne Edwards).<sup>2</sup> In *Sesarma magdalenense*, however, the inner orbital lobe, although large, does not meet the angle of the front and exclude the antenna from the orbit.

#### GEARCINIDÆ

##### *Cardisoma crassum* Smith

1870, Trans. Connecticut Acad. Arts and Sci., II, p. 144, Pl. v.

Agua Verde Bay; 1 ♀.

#### OCYPODIDÆ

##### *Ocypode occidentalis* Stimpson

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 229.

Cape St. Lucas; March 23; 3 ♂.

Carmen Island: with 175-foot seine; April 3; 3 ♂ 3 ♀. April 7; 2 ♂.

##### *Uca crenulata* (Lockington)

*Gelasimus crenulatus* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876, p. 149.

Mangrove Island, Magdalena Bay; March 20, 1911; 4 ♂.

Agua Verde Bay; April 2; 1 ♂.

Head of Concepcion Bay; April 6; 13 ♂.

<sup>1</sup>1853, Ann. Sci. Nat., Zoöl., (3) XX, p. 188 [154].

<sup>2</sup>*Sesarma* (*Holometopus*) *aubryi* A. Milne Edwards, 1869, Nouv. Arch. Mus. Hist. Nat. Paris, V, p. 29.



**PARTHENOPIDÆ****Heterocrypta macrobrachia** Stimpson

1871, Ann. Lyc. Nat. Hist. N. Y., X, p. 103.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20'' N., long. 111° 59' 35'' W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 1 juv.

**MAJIDÆ** (= Inachidæ)**Stenorynchus debilis** (Smith)

*Leptopodia debilis* SMITH, 1871, Rept. Peabody Acad. Sci., 1869, p. 87.

Without locality label; 1 ovigerous ♀.

**Podochela hemphillii** (Lockington)

*Microhynchus hemphillii* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876, p. 30 [3].

San Estaban Island; April 14; 1 ♂.

"Station D5679"; 1 ♂. As the depth at this station is 325 fathoms, the label is probably erroneous.

**Eucinetops panamensis** Rathbun

1923, Proc. Biol. Soc. Washington, XXXVI, p. 73.

San Francisquito Bay; beach; April 9; 1 ♂, soft-shell.

**Euprognatha bifida** Rathbun

1893, Proc. U. S. Nat. Mus., XVI, p. 231.

Middle of east side of Cerros Island; March 12; 3 ♂ 2 ♀.

**Collodes granosus** Stimpson

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 194 [66], Pl. II, fig. 4.

Cape San Lucas; March 23; 1 ovigerous ♀.

**Collodes tumidus** Rathbun

1898, Proc. U. S. Nat. Mus., XXI, p. 569, Pl. XLI, fig. 1.

Middle of east side of Cerros Island; March 12; 1 ♀ juv.

**Inachoides tuberculatus** (Lockington)

*Inachus tuberculatus* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, p. 30.

Santa Maria Bay; with boat dredge; March 18; 1 ♂ 4 ♀.

Without locality label; 3 ♂ 3 ♀.



***Epialtus sulcirostris* Stimpson**

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 198 [70].

Santa Maria Bay; with boat dredge; March 18; 1 ♂.

***Epialtus nuttallii* (Randall)**

*Libinia nuttallii* RANDALL, 1840, Journ. Acad. Nat. Sci. Philadelphia, VIII, 1839, Pl. III.

W. San Benito Island; March 9; 1 ♀ juv.

***Loxorhynchus grandis* Stimpson**

1857, Proc. Boston Soc. Nat. Hist., VI, p. 85.

Point San Bartholome; 1 ♀. This is farther south than the species has hitherto been recorded.

***Chorilia longipes* Dana**

1851, Amer. Journ. Sci., (2) XI, p. 269.

W. of Point Buchon, California: Pine Mountain, N. 42° E.; lat. 35° 18' 30'' N., long. 121° 28' W.; 440 fathoms; temp. 39.9° F.; April 27; station D5696; 1 ♂ 1 ♀.

W. of San Nicolas Island, California: lat. 33° 13' 30'' N., long. 120° 04' 30'' W.; 451 fathoms; April 26; station D5693; 4 ♂ 3 ♀.

***Chionoecetes tanneri* Rathbun**

1893, Proc. U. S. Nat. Mus., XVI, p. 76, Pl. iv, figs. 1-4.

Taken at the following localities off the California coast:

Off Carmelo Bay: lat. 36° 30' N., long. 122° W.; 659 fathoms; gn. M.; temp. 37.9° F.; April 27; station D5699; 7 ♂ 9 ♀.

Off Point Sur: Point Sur, N. 6° W.; Juniperro Mountain, N. 47° E.; lat. 35° 50' N., long. 121° 49' 30'' W.; 475 fathoms; temp. 39.9° F.; April 27; station D5698; 8 juv.

W. of Piedras Blanca: Silver Peak, N. 40° E.; Pine Mountain, N. 75° E.; lat. 35° 35' N., long. 121° 39.8' W.; 485 fathoms; gn. M. bk. S.; temp. 39.8° F.; April 27; station D5697; 14 juv.

W. of Point Buchon: Pine Mountain, N. 42° E.; lat. 35° 18' 30'' N., long. 121° 28' W.; 440 fathoms; temp. 39.9° F.; April 27; station D5696; 2 large ovigerous ♀, 2 ♂, 3 ♀ immature, and 16 juv.

N. W. of San Nicolas Island: lat. 33° 33' N., long. 120° 17' 30'' W.; 534 fathoms; gn. S. Glob.; temp. 38.9° F.; April 26; station D5695; 1 large ♂, 4 juv.

N. W. of San Nicolas Island: lat. 33° 24' 36'' N., long. 120° 12' 30'' W.; 640 fathoms; gn. M.; April 26; station D5694; 1 immature ♀, 1 juv.



The specimens are of various sizes and have very slender spines on the margins and also in the two dorsal branchial lines, one transverse, the other oblique. The slender meropodites of the legs are very narrow, not at all dilated, although tapering gradually to the distal end and are bristling with sharp spines especially on both margins.

Length of largest specimen (male) on median line 124.4 mm., width between lower branchial margins (finely spined) 135 mm.

***Libinia setosa* Lockington**

1877, Proc. California Acad. Sci., VII, 1876, p. 68 [6].

Santa Maria Bay; with boat dredge; March 18; 1 ♂ 2 ♀ 13 juv.  
Without locality label; 4 juv.

***Thoe sulcata* Stimpson**

1860, Ann. Lyc. Nat. Hist. N. Y., VII, p. 177.

San Francisquito Bay; beach; April 9; 1 ♂.

***Pitho picteti* (Saussure)**

*Othonia picteti* SAUSSURE, 1853, Rev. et Mag. de Zool., (2) V, p. 357, Pl. XIII, fig. 2.

Without locality label; 1 ♂.

***Mithrax sinensis* Rathbun**

1892, Proc. U. S. Nat. Mus., XV, p. 266, Pl. XXXVIII, fig. 2.

San Estaban Island; 1 ♂.

***Stenocionops triangulata* (Rathbun)**

*Pericera triangulata* RATHBUN, 1892, Proc. U. S. Nat. Mus., XV, p. 246, Pl. XXXII, fig. 1.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5 fathoms; S. brk. Sh.; March 21; station D5678; 1 ♀ juv.

***Microphrys triangulatus* (Lockington)**

*Mithraculus triangulatus* LOCKINGTON, 1877, Proc. California Acad. Sci., VII, 1876, p. 73 [11].

San Josef Island; March 31; 1 ♂.

Agua Verde Bay; April 2; 1 ♂.

Without locality label; 1 ♂.

***Microphrys branchialis* Rathbun**

1898, Proc. U. S. Nat. Mus., XXI, p. 577, Pl. XLI, fig. 5.

Magdalena Bay: Sail Rock, Entrada Point, S. 53° W.; Redondo Point, S. 15° W.; lat. 24° 35' 20" N., long. 111° 59' 35" W.; 13.5



fathoms; S. brk. Sh.; March 21; station D5678; 1 immature ♂, the chelipeds slightly developed, scarcely larger than the first ambulatory leg.

#### LIST OF LARVAL FORMS

##### *Dromidia larraburei*

Cape San Lucas, ship's anchorage, taken by electric light; one megalops, 5 mm. long. (See Pl. XXXIII, fig. 4.)

Point San Bartholome; one megalops, lacking chelipeds.

Middle of east side of Cerros Island, March 12, one female, early postlarval stage.

As *D. larraburei* is the only dromiid in the region, the identification of the above is reasonably certain.

Carmen Island, southeast side, taken by electric light; one megalops, 2.9 mm. long. (See Pl. XXXIII, fig. 3.) This and the following forms are placed under *Dromidia* on account of the great development of the coxa of the hind legs.

Cape San Lucas; 5 megalopa, 3 mm. long. (See Pl. XXXIII, figs. 1 and 2.)

##### *Callinectes*

Cape San Lucas; 50+ megalopa, 5 mm. long. (See Pl. XXXVI, fig. 3.)

Cape San Lucas; 50+ megalopa, of two sizes. Seem to be the same as the figured lot.

Carmen Island, southeast side, taken by electric light; 50+ megalopa. Perhaps same as the two preceding lots.

San Francisquito Bay, taken by electric light; about 10 megalopa, with legs broken off. Perhaps belong here.

There are three species of *Callinectes* in the region; *arcuatus*, *toxotes* and *bellicosus*. The first two were described from Cape San Lucas; *bellicosus* is as near the Cape as La Paz on the one side and Magdalena Bay on the other. According to Dr. Fish, the megalopa figured is almost identical with that of *Callinectes sapidus* of the Atlantic coast.

##### Portunidæ, genus unknown, perhaps *Callinectes*

Cape San Lucas; 3 megalopa, 6.6 mm. long. (See Pl. XXXVI, fig. 4.)

##### *Pliosoma* (?), or *Libinia* (?)

Carmen Island, southeast side; one megalops, 2.2 mm. long. (See Pl. XXXVI, fig. 2.) Dr. Fish says that this closely resembles an Atlantic species of *Libinia*.

##### *Pachygrapsus crassipes* (?)

Cape San Lucas; one megalops.

Guadalupe Island, taken by electric light, March 3; 25+ megalopa, 6 mm. long. (See Pl. XXXIV, figs. 1 and 2.) The large size indicates a large species of Grapsoid.

##### *Sesarma (Holometopus) magdalenense*

Carmen Island, southeast side, taken by electric light; one megalops.



Cape San Lucas; 3 megalopa, 5.5 mm. long. (See Pl. XXXIV, figs. 3-5.)

Cape San Lucas, ship's anchorage, taken by electric light; 5 megalopa.

The larvæ show (Pl. XXXIV, fig. 5) the humped movable finger peculiar to *S. magdalenense* (Pl. XXXII).

Grapsoid. A pair of pigment spots on each abdominal somite.

Point San Bartholome; one megalops.

Benito Island; 6 megalopa, 5 mm. long. (See Pl. XXXV, figs. 4-6.)

Grapsoid, different from the preceding. Body thick, color reddish in alcohol, speckled.

Cape San Lucas; 20 megalopa, 2.3 mm. long. (See Pl. XXXV, figs. 1-3.)

### *Libinia setosa*

Cape San Lucas; 4 megalopa, 3.15 mm. long. (See Pl. XXXVI, fig. 1.) Dr.

Fish says that this is very similar to an Atlantic species of *Libinia*, the rostrum of which is more pointed. The only *Libinia* known from Cape San Lucas is *L. setosa*. Another Mexican form, *L. mexicana*, has been taken only at the extreme head of the Gulf of California.



PLATE XXVI

*Pliosoma parvifrons*

- Fig. 1. Cape San Lucas, ♂, carapace 20 mm. long, dorsal view.  
Fig. 2. Same specimen, ventral view.







PLATE XXVII

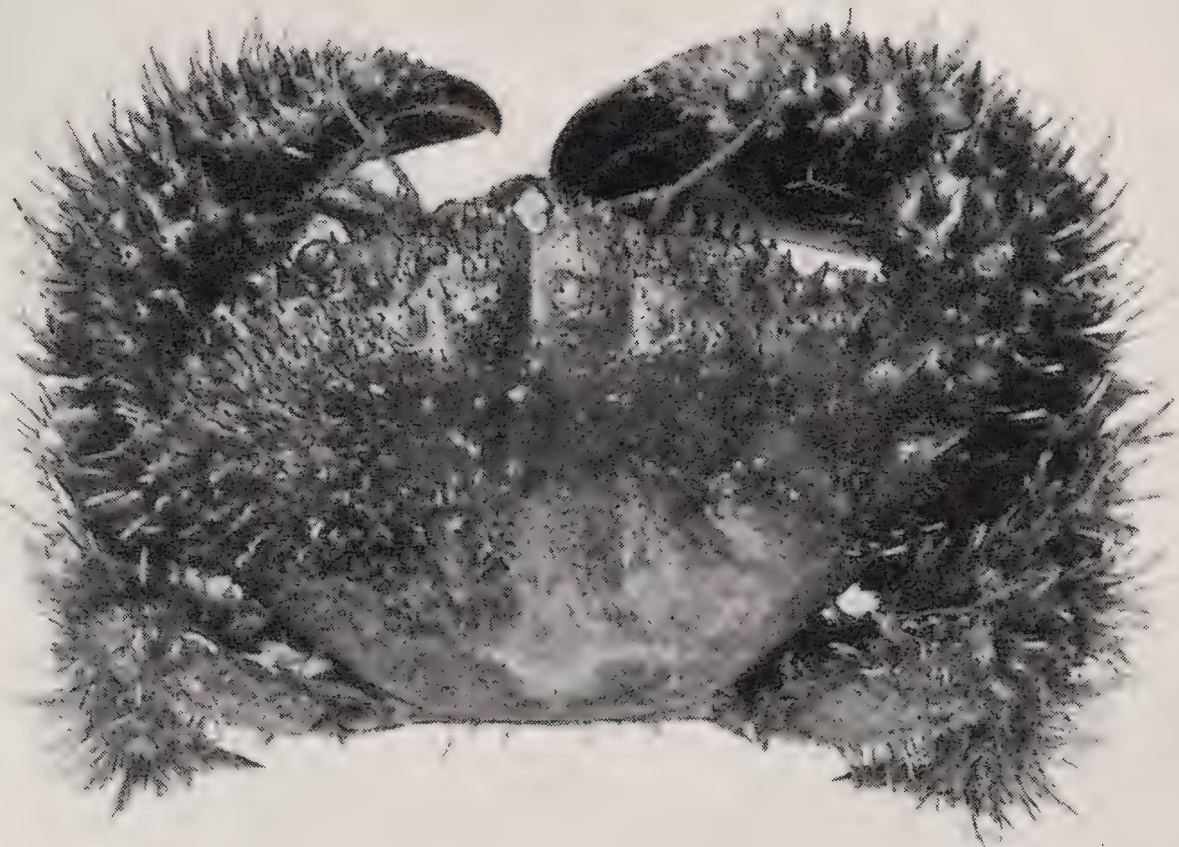
*Pilumnus spinohirsutus*

Fig. 1. Female (Cat. No. 54763, U. S. N. M.), carapace 17.2 mm. long, dorsal view.

Fig. 2. Same specimen, ventral view.



1



2

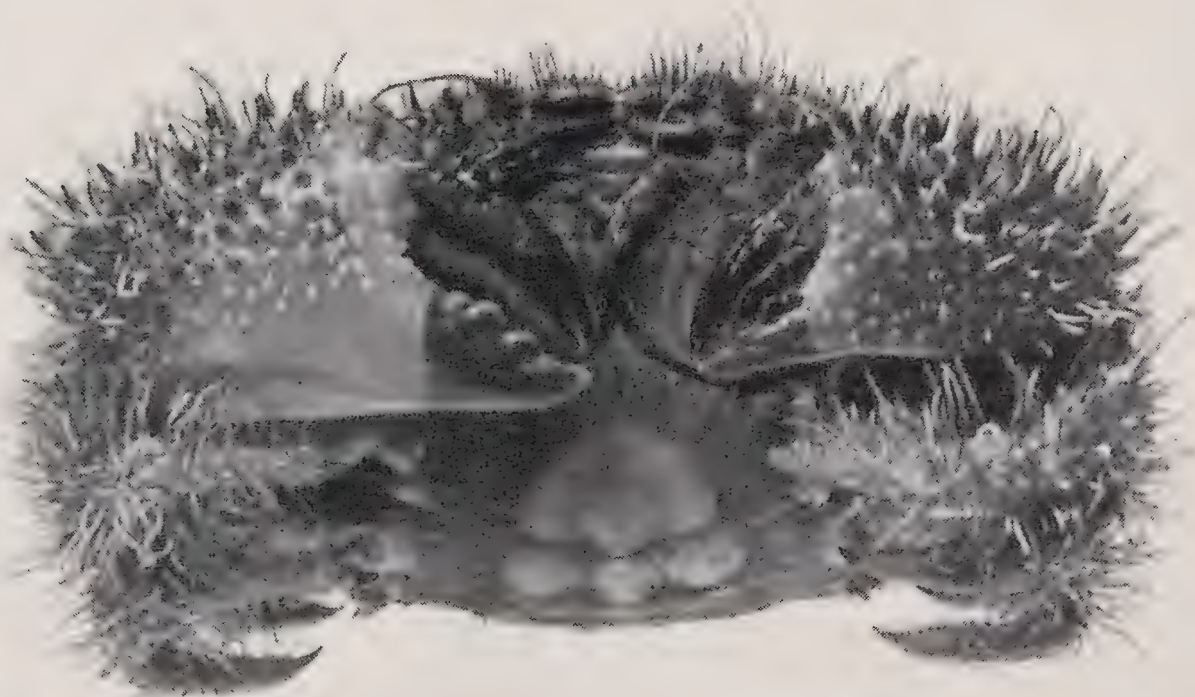




PLATE XXVIII

*Pilumnus townsendi*

Fig. 1. Female holotype, carapace 13.8 mm. long, dorsal view. The second lateral tooth counting from the orbit is below the margin of the carapace.

Fig. 2. Same specimen, ventral view.



1



2





PLATE XXIX

*Pinnotheres jamesi*

Fig. 1. Male holotype, carapace 3.7 mm. long, dorsal view.

Fig. 2. Same specimen, ventral view.



1



2





PLATE XXX

*Pinnotheres pichilinguei*

- Fig. 1. Male holotype, carapace 4.4 mm. long, dorsal view.  
Fig. 2. Same specimen, ventral view, to show abdomen.  
Fig. 3. Same specimen, ventral view, to show chelæ.



1



2



3





PLATE XXXI

*Goetice americanus*

Fig. 1. Male, Guaymas (Cat. No. 17292, U. S. N. M.), carapace 10 mm. long, dorsal view.

Fig. 2. Same specimen, ventral view.



1



2





PLATE XXXII

*Sesarma (Holometopus) magdalenense*

Photographs lent by U. S. National Museum

- Fig. 1. Male holotype, carapace 11.6 mm. long, anterior view.
- Fig. 2. Same specimen, dorsal view.
- Fig. 3. Same specimen, ventral view.



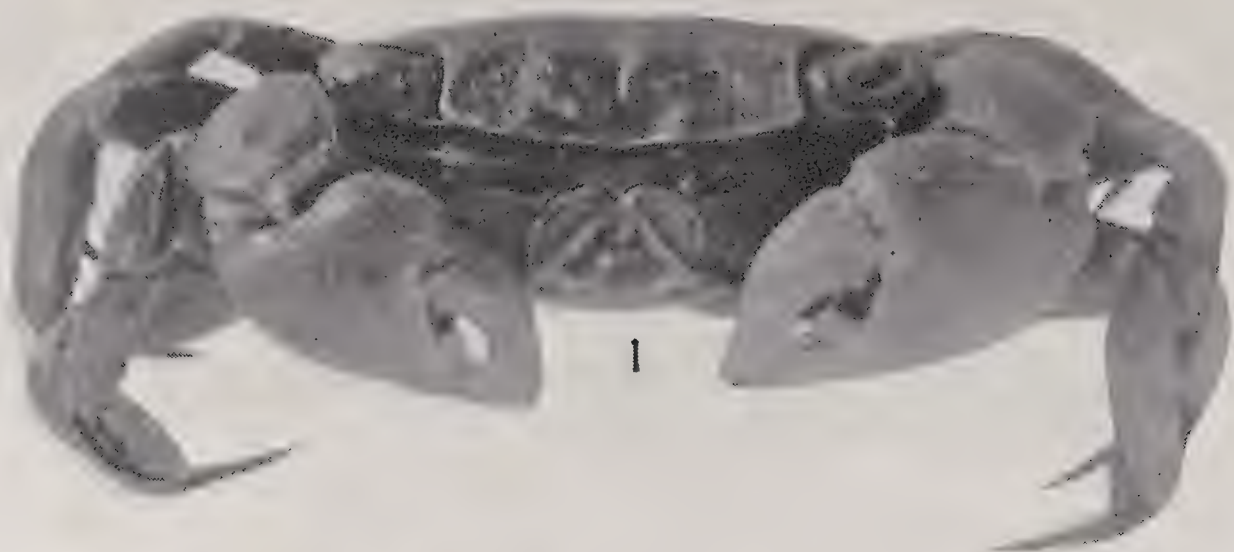




PLATE XXXIII

*Dromidia larraburei*

- Fig. 1. Megalops, Cape San Lucas, carapace 3 mm. long, dorsal view.
- Fig. 2. Left cheliped of Fig. 1.
- Fig. 3. Megalops, Carmen Island, carapace 2.9 mm. long, dorsal view.
- Fig. 4. Megalops, Cape San Lucas, carapace 5 mm. long, dorsal view.



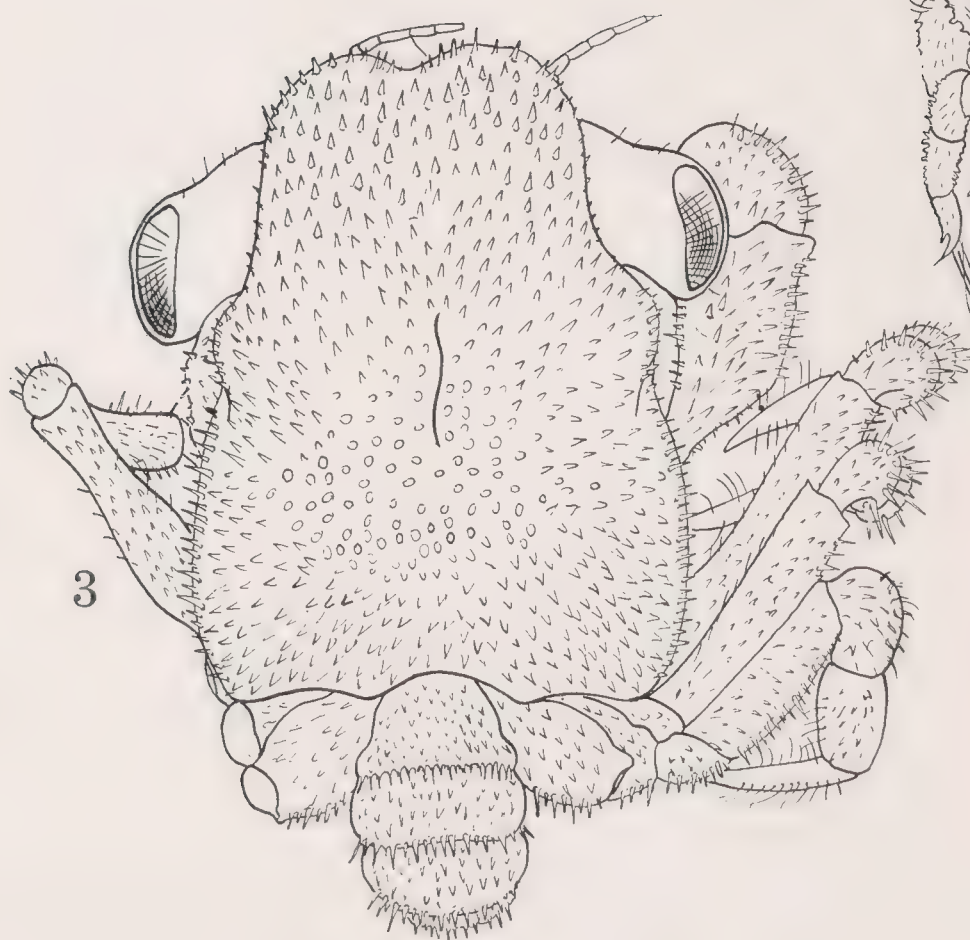
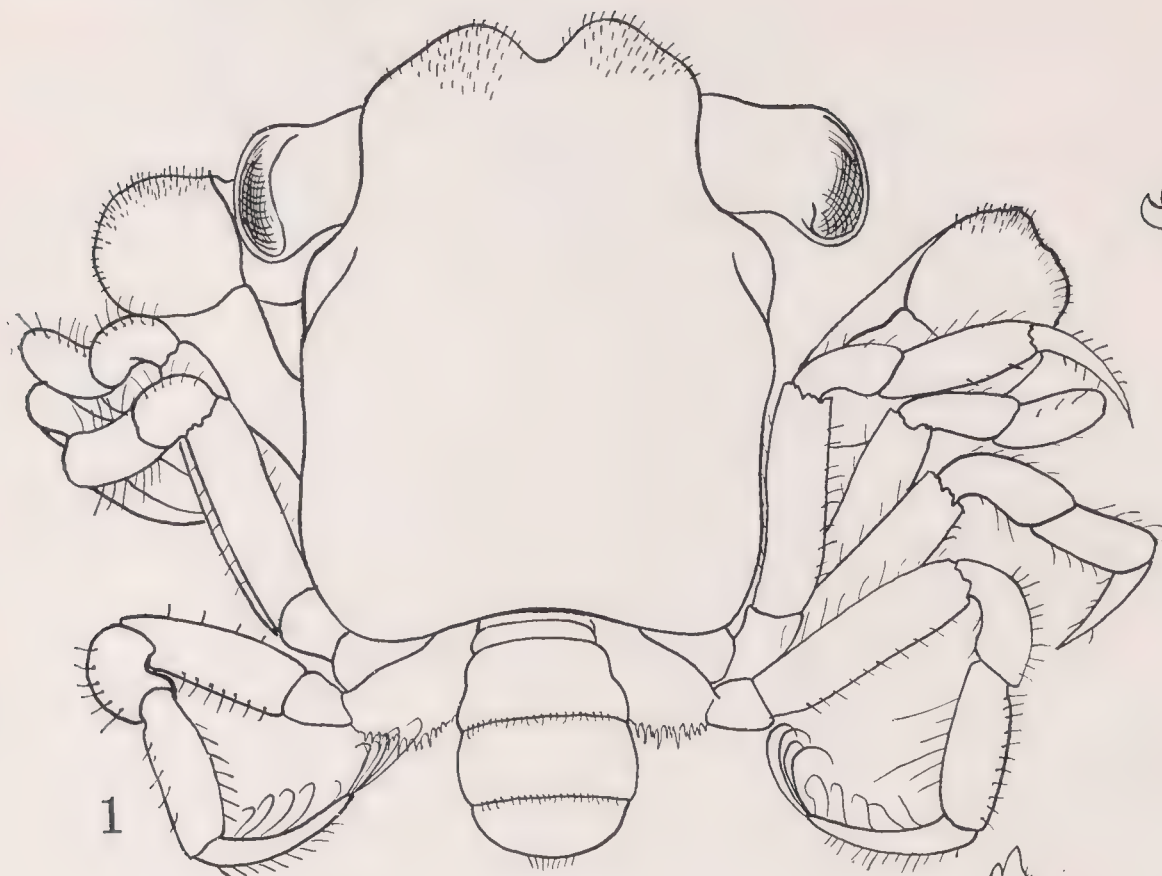




PLATE XXXIV

Fig. 1. *Pachygrapsus crassipes* (?), megalops, Guadalupe Island, carapace 6 mm. long, dorsal view.

Fig. 2. Front view of Fig. 1.

Fig. 3. *Sesarma magdalenensis*, megalops, Cape San Lucas, carapace 5.5 mm. long, dorsal view.

Fig. 4. Front view of Fig. 3.

Fig. 5. Left cheliped of Figs. 3 and 4.



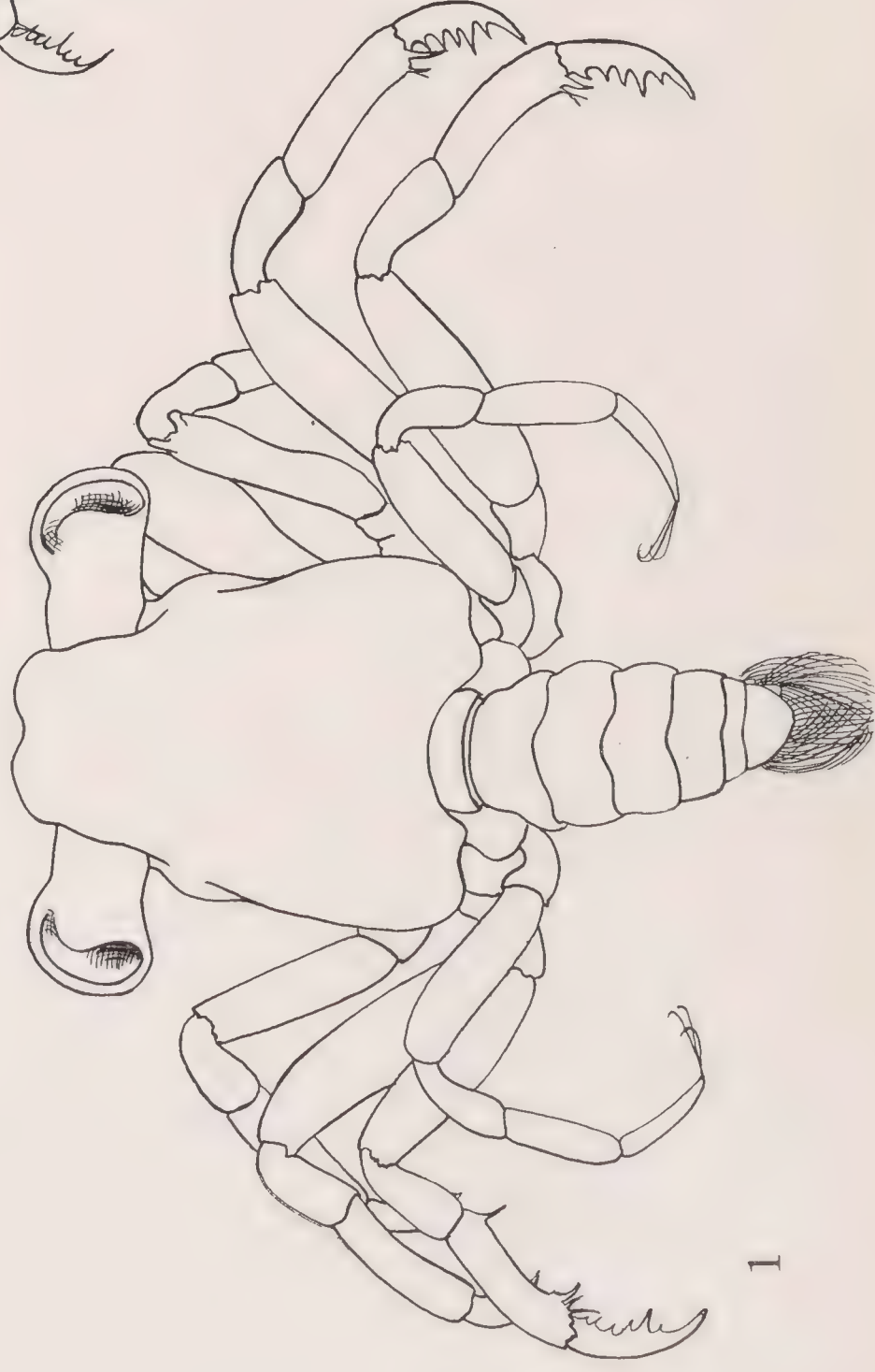




PLATE XXXV

Fig. 1. Grapsoid, megalops, Cape San Lucas, carapace 2.3 mm. long, dorsal view.

Fig. 2. Right cheliped of Fig. 1.

Fig. 3. Front view of Fig. 1.

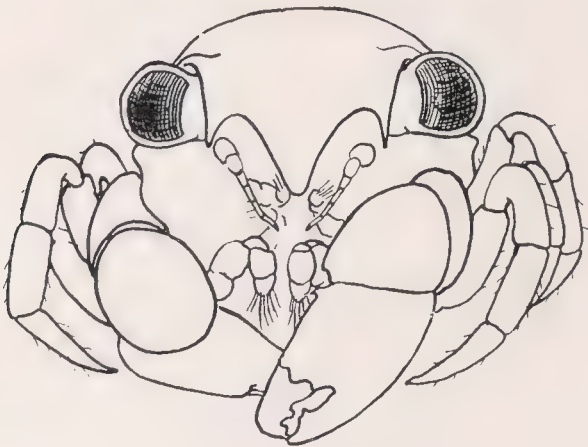
Fig. 4. Grapsoid, megalops, unlike Fig. 1, Benito Island, carapace 5 mm. long, dorsal view.

Fig. 5. Left cheliped of Fig. 4.

Fig. 6. Front view of Fig. 4.



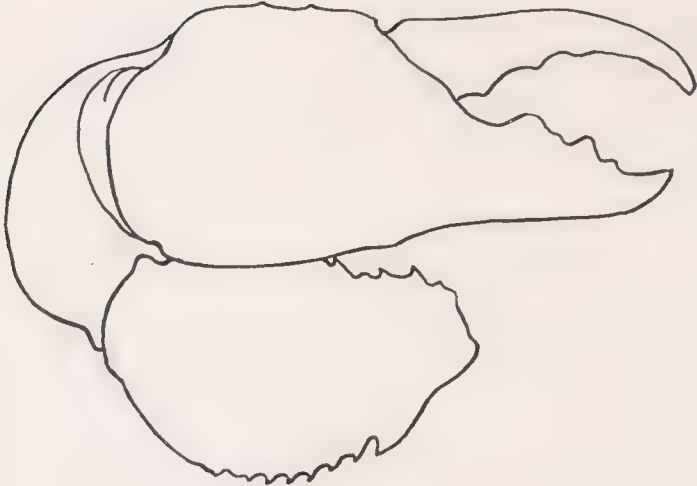
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6



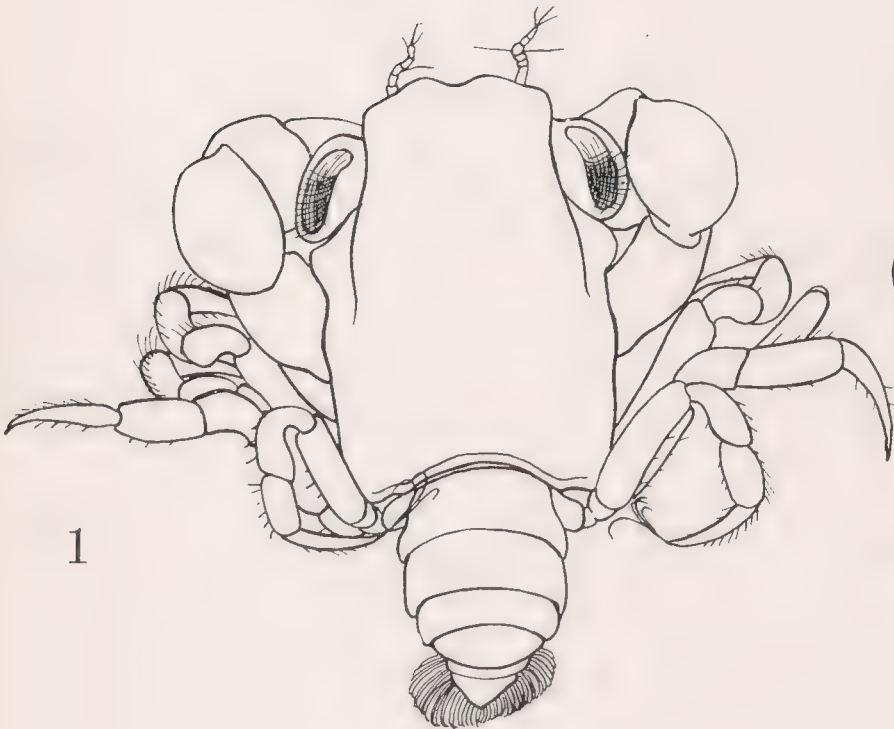
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1



4

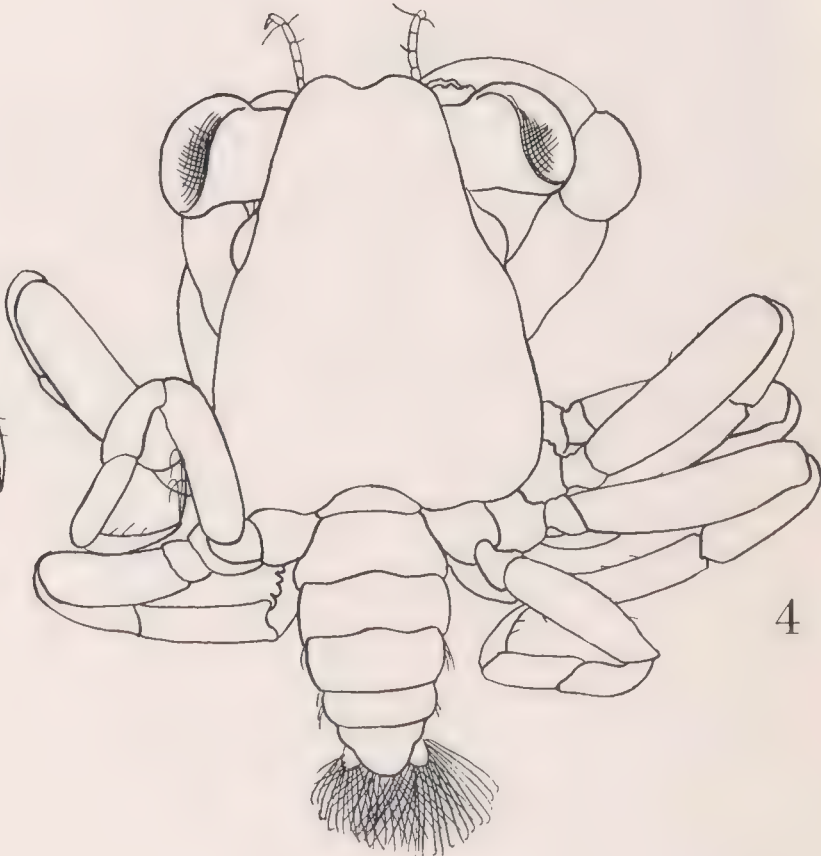




PLATE XXXVI

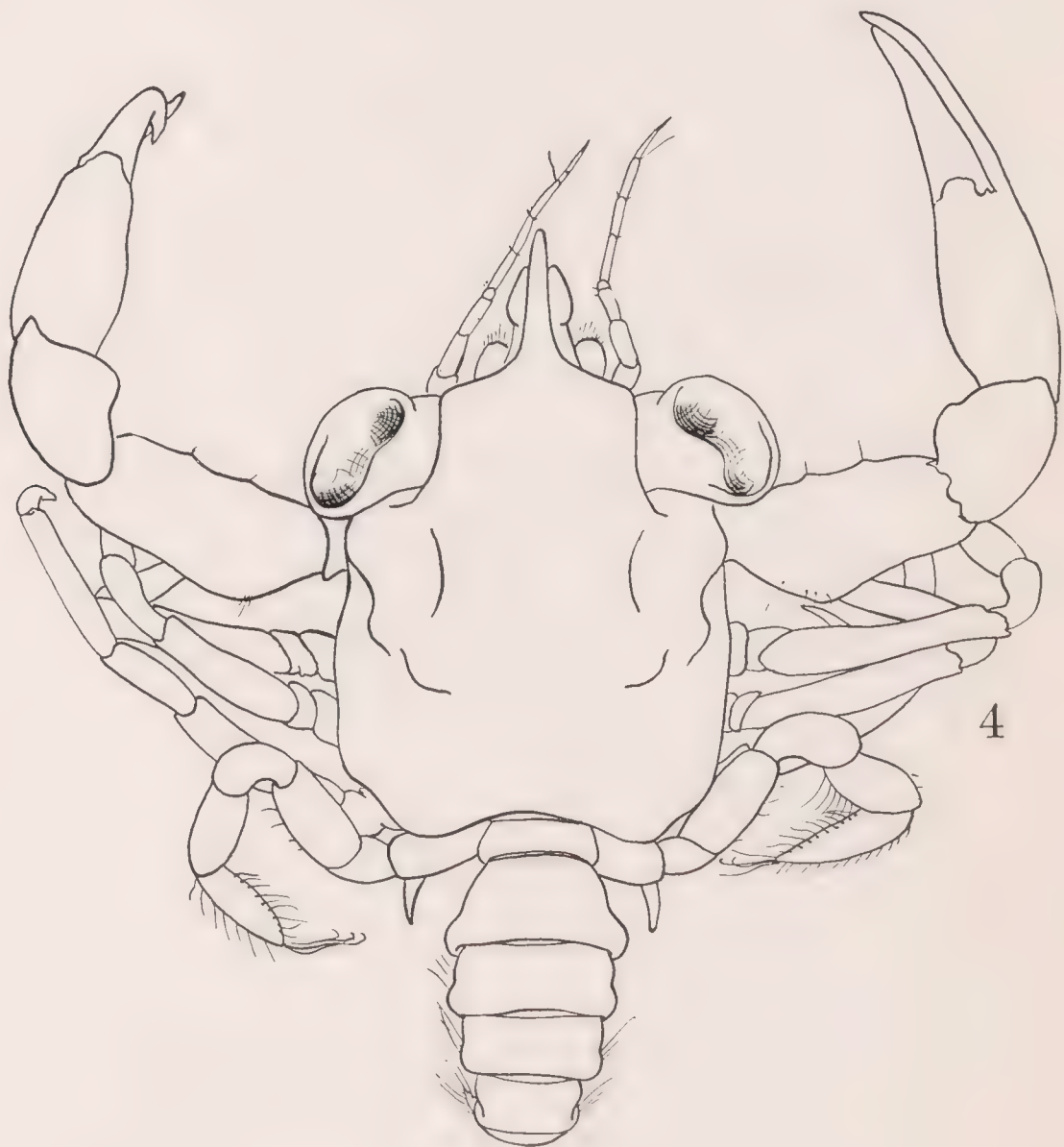
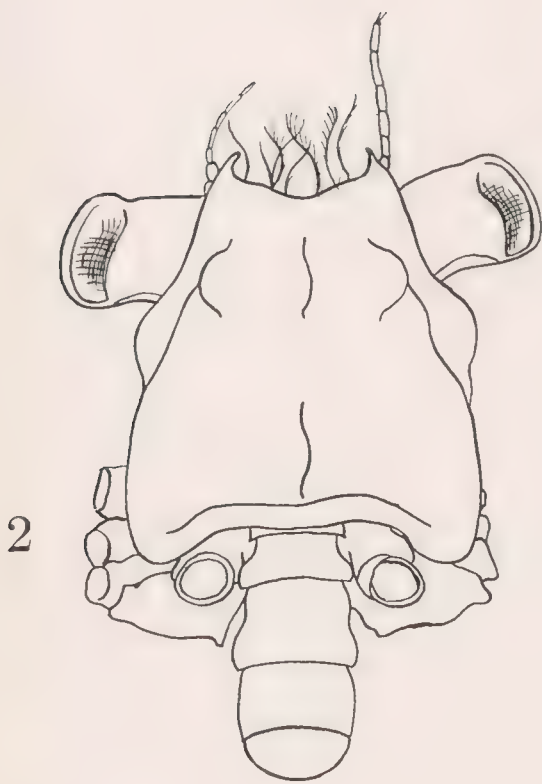
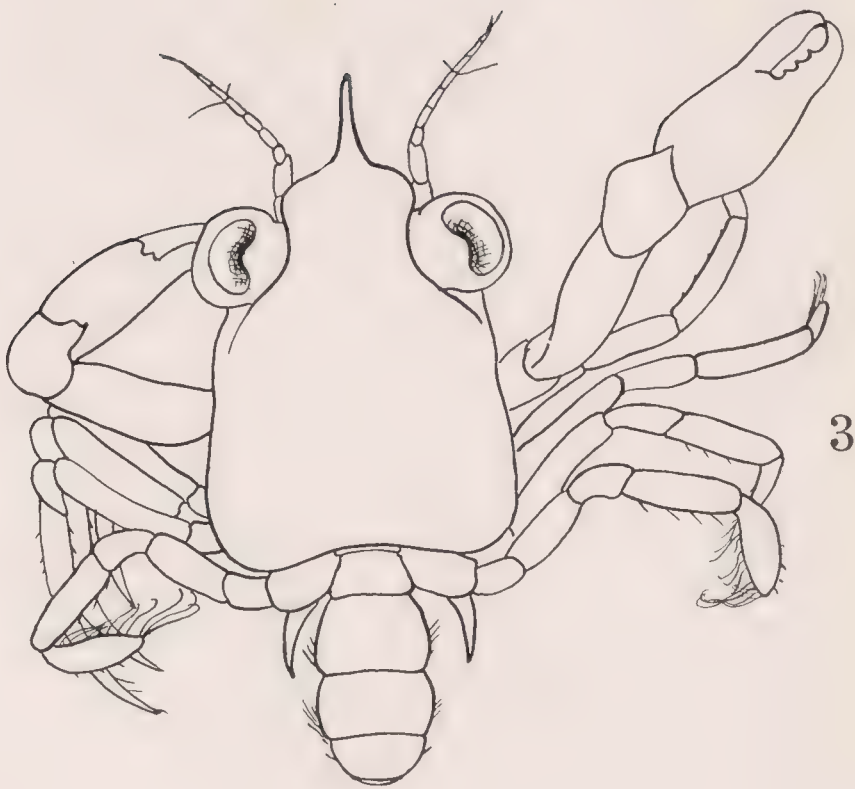
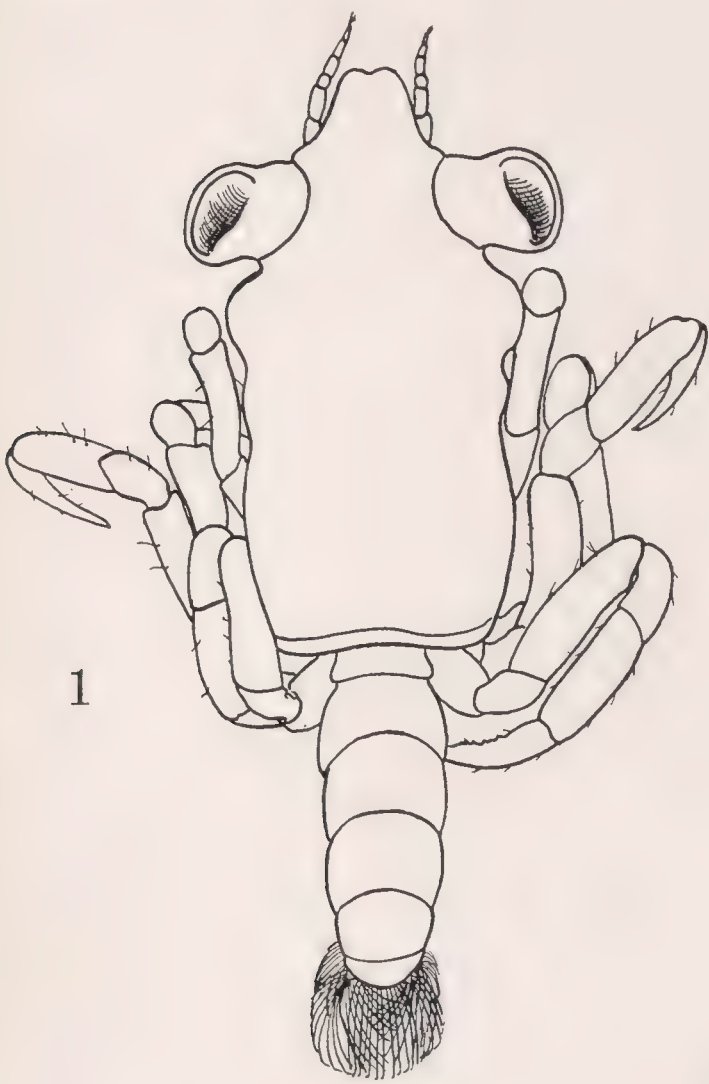
Fig. 1. *Libinia setosa*, megalops, Cape San Lucas, carapace 3.15 mm. long, dorsal view.

Fig. 2. *Pliosoma*, megalops, Carmen Island, carapace 2.2 mm. long, dorsal view.

Fig. 3. *Callinectes*, megalops, Cape San Lucas, carapace 5 mm. long, dorsal view.

Fig. 4. Portunid, megalops, Cape San Lucas, carapace 6.6 mm. long, dorsal view.











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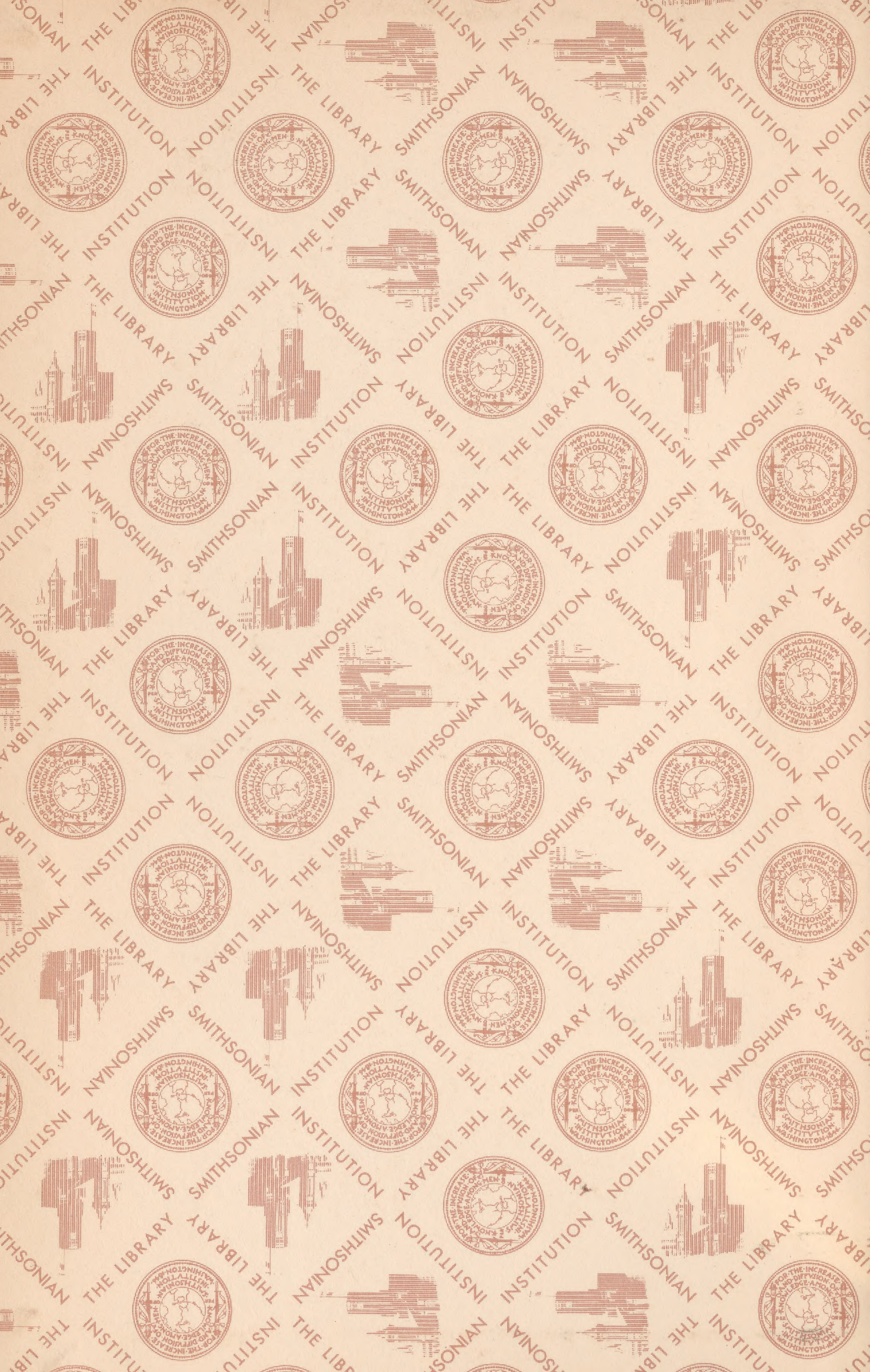




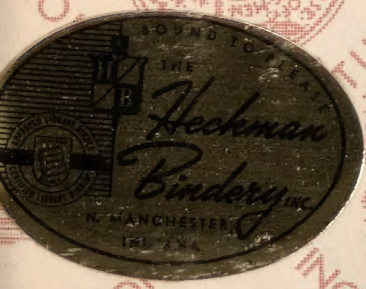














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